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A SIMPLIFIED METHOD OF CONSTRUCTING MERCHANTABLE BOARD-FOOT VOLUME TABLES[1]

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INTRODUCTION

Several methods of preparing tables to show the merchantable contents of standing trees in board feet, or in some other unit of measure, are in customary use. All these methods have two disadvantages in common: They require large numbers of detailed field measurements; and the computation of tables by any of them is a rather lengthy and difficult process, particularly for anyone not specially trained in mensuration.

In addition to the difficulties of preparation, the tables themselves have certain shortcomings. Two basic types of merchantable board-foot volume tables are most often used. The first type relates volume to diameter at breast height and at total height of the tree; the second is based on diameter at breast height and "merchantable height", or the distance from the ground to a point on the trunk of the tree with a given fixed diameter. In the first type of table, although the volume is based on total height, the actual volume given is that of the trunk up to a point of fixed top diameter. In both types, therefore, the point of merchantability is actually determined solely by minimum diameter. This is a disadvantage, because in actual utilization merchantability is much more often limited by the presence of large limbs or deformities of the bole (particularly in hardwoods).

The second type of table has the additional disadvantage of being difficult to use correctly in the field, because of the necessity of estimating the point on the trunk, usually quite high above ground, where the fixed top diameter occurs.

A method of preparing volume tables which takes into account the fact that the position of large branches and irregularities of the bole more often determine the actual upper limit of merchantability than does an assumed minimum diameter, would seem to have practical advantages. Such a method is described in this paper.

FACTORS INFLUENCING VOLUME DIFFERENCES AMONG SPECIES

The common practice in forest mensuration is to use a different volume table for each species and sometimes even for the same species in different localities. It may be assumed, therefore, that the correlation between the dependent variable, volume, and the two independent variables, diameter and height, is definitely affected by species, for if all trees had the same form, the same bark thickness, and the same degree of butt swell, volume would vary with height and diam-

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eter in exactly the same way for all species. Within species these factors are relatively constant, and in some cases a number of species are so similar as to permit of grouping.

Numerical expressions for these several factors were worked out in this study for 14 species from three forest regions. By using these expressions it was possible actually to measure the difference between species. A single basic correlation of volume with diameter and height was determined. This can be modified by the use of these numerical expressions so that it will fit any species or particular sample of a species.

BARK THICKNESS

The first factor which causes a difference between species is bark thickness. The diameter measurement upon which the volume estimate is based is made outside the bark, while the volume is measured inside the bark. Thus it is clearly evident that, if the bark of one species averages 10 percent of the diameter and the bark of a second species is 7 percent of the diameter, the correlation between volume and diameter for each of the species will be different. In order to eliminate this factor as a source of difference between species, the diameter breast high [2] used in the basic correlation of volume with diameter and height is measured, in this method, inside the bark instead of outside.

BUTT SWELL

Another factor which is fairly constant within a species but different between species is butt swell, which affects the measurement of diameter at breast height. Trees with a large degree of butt swell have less volume for a given diameter than do trees with only a slight degree. A satisfactory numerical measure of butt swell was found to be afforded by the ratio of the diameter at 18.3 feet above the ground (top of first 16.3-foot log above a 2-foot stump) to the diameter at breast height, both measurements being made inside the bark.[3] This factor is denoted as *B*. It is relatively constant within a species, at least within rather broad geographical limits. Table 1 shows the average value of *B* and its standard deviation for a number of species.

TABLE 1.—*Average value and standard deviation of B (butt swell factor), by species*

Species	Average value of *B*	Standard deviation	Trees	Species	Average value of *B*	Standard deviation	Trees
Hardwoods:			*Number*	Conifers:			*Number*
Basswood (*Tilia glabra* Vent.)	0.83	0.054	275	Balsam fir (*Abies balsamea* (L.) Mill.)	.81	.047	81
Beech (*Fagus grandifolia* Ehrh.)	.86	.043	339	Hemlock (*Tsuga canadensis* (L.) Carr.)	.85	.041	240
Elm (*Ulmus americana* L.)	.84	.048	140	Jack pine (*Pinus banksiana* Lamb.)	.86	.042	57
Red gum (*Liquidambar styraciflua* L.)	.81	.046	119	Loblolly pine (*P. taeda* L.)	.90	.046	106
Red maple (*Acer rubrum* L.)	.84	.037	131	Norway pine (*P. resinosa* Ait.)	.90	.073	186
Sugar maple (*A. saccharum* Marsh.)	.86	.046	553	Shortleaf pine (*P. echinata* Mill.)	.91	.037	59
Yellow birch (*Betula lutea* Michx. f.)	.84	.040	296	White pine (*P. strobus* L.)	.88	.034	80

[2] 4.5 feet above ground level.

[3] This factor was suggested by a form-class measurement developed by J. W. Girard, but differs in that in this case both measurements are taken inside the bark; in Girard's form class, the measurement at top of first log is inside bark, but diameter breast high is measured outside bark.

FORM

Form or taper in the upper part of the bole is a third factor which causes variation in volume between species. Several numerical measures of the form of trees have been devised, the most common of which is the ratio of the diameter at half the height of the tree to the diameter at breast height. Several minor modifications of this form quotient have also been used. These expressions of form all have the same weakness—the basic measurement is diameter breast high, and since diameter at breast height is often affected by butt swell, the form quotient is likewise influenced by the degree of butt swell whereas it should vary solely with taper. In this analysis a factor was found which avoids this source of variation. This is the ratio of the diameter inside bark at 34.6 feet [4] above ground to the diameter inside bark at 18.3 feet above ground, hereafter denoted as D. Table 2 shows the average value and standard deviation of D for a number of species.

TABLE 2.—*Average value and standard deviation of D (factor of form), by species*

Species	Average value of D	Standard deviation	Trees	Species	Average value of D	Standard deviation	Trees
Hardwoods:			*Number*	Conifers:			*Number*
Basswood	0.89	0.040	275	Hemlock	0.86	0.072	221
Beech	.89	.038	219	Jack pine	.82	.057	57
Red gum	.87	.047	119	Loblolly pine	.87	.041	106
Sugar maple	.89	.041	377	Norway pine	.89	.074	187
Yellow birch	.87	.041	157	Shortleaf pine	.85	.048	59
				White pine	.91	.038	80

By controlling these three factors, bark thickness, butt swell (B), and form (D), it was possible to determine a correlation between volume and diameter which is constant for all species.

THE BASIC CURVES OF VOLUME

Stem measurements of approximately 2,000 trees were used in developing the set of curves which is the basis for the system of volume-table construction presented. These trees were first classified by log lengths. The trees in each log-length class were then sorted into D classes and subsorted into B classes. Thus, in the final grouping, log length, D, and B were all constant within a classification interval. Merchantable volume in board feet was then plotted over diameter breast high inside bark with a separate curve plotted for each of the final groups. In effect, these curves represent the correlation of volume with diameter breast high inside bark, with the other factors (butt swell and form) held constant—in statistical terms, the net regression of volume with diameter breast high inside bark.

Within each log class, the curves were parallel and in logical order one above the other, indicating that there was no joint relationship between volume and the three variables, diameter breast high, B, and D. Therefore, a single curve was drawn for each log class, parallel to the average trend of the series for that log class and through the ordinates which represented the average values of B and D. The final set of curves is illustrated in figures 1 to 5.

[4] Equal to two 16-foot logs plus trimming allowance and a 2-foot stump.

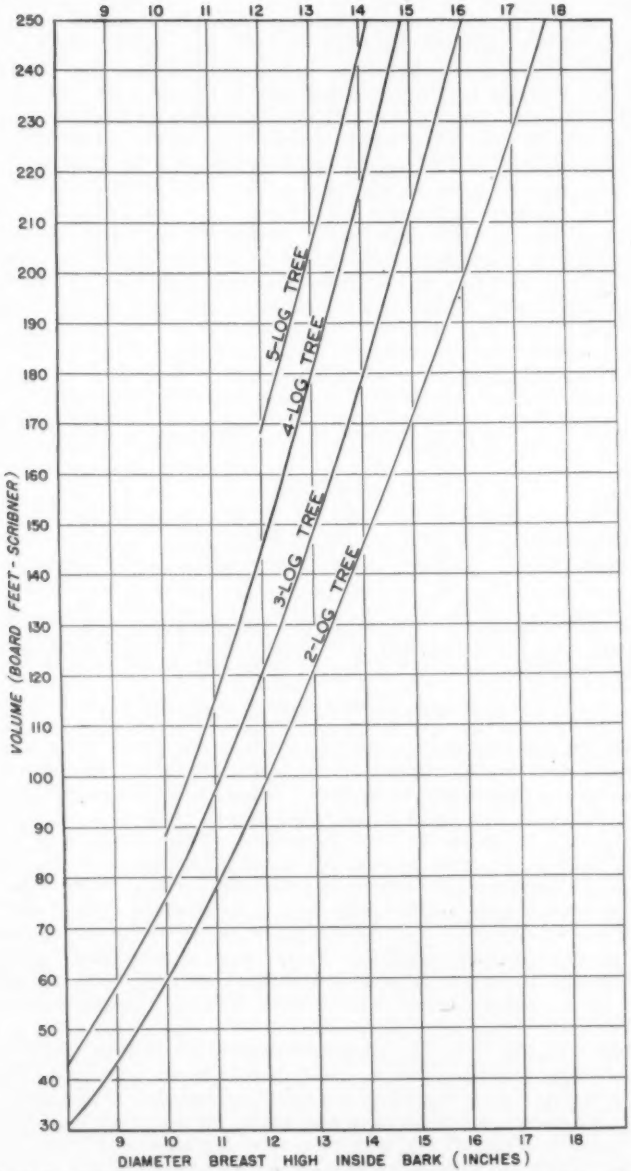


FIGURE 1.—Correlation of volume with diameter breast high inside bark. (30 to 250 board feet.)

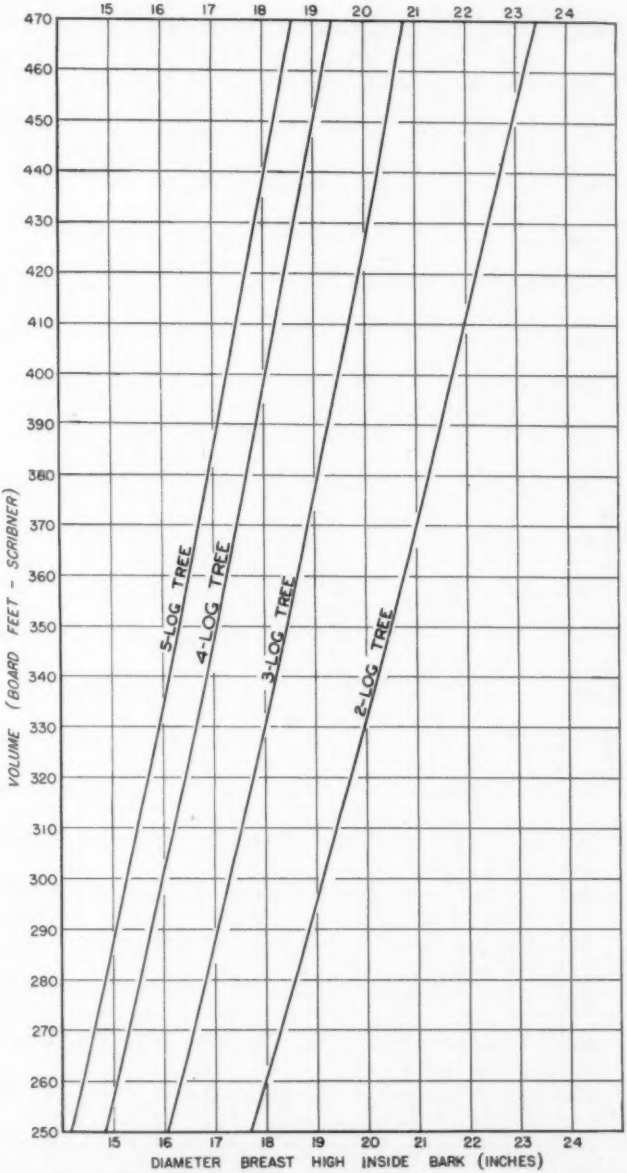


FIGURE 2.—Correlation of volume with diameter breast high inside bark. (250 to 470 board feet.)

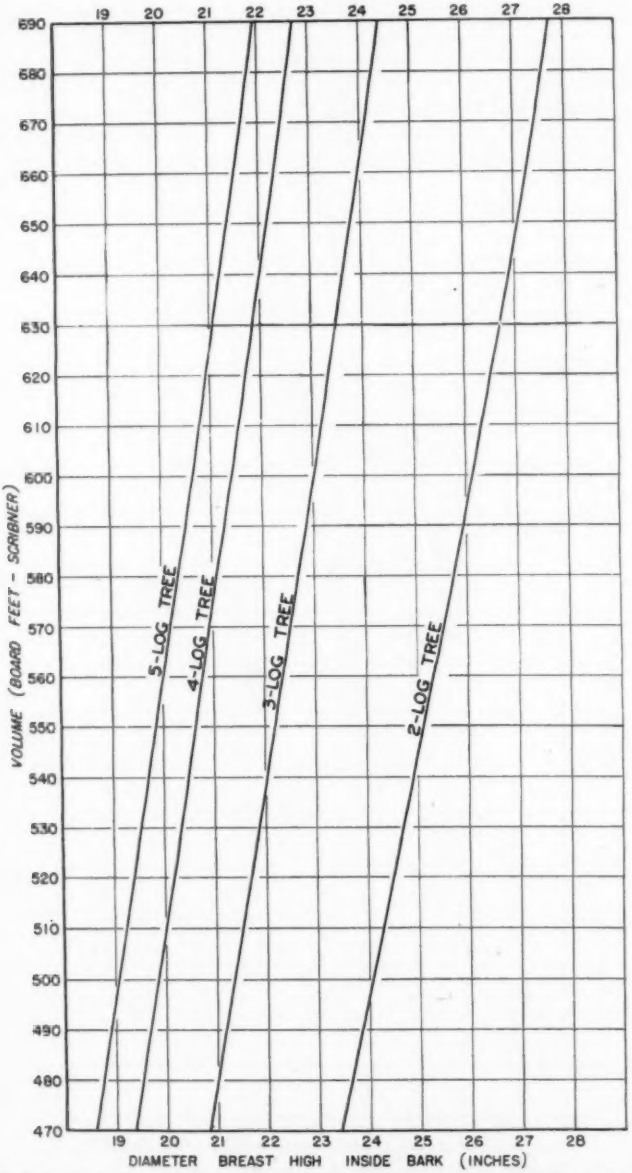


FIGURE 3.—Correlation of volume with diameter breast high inside bark. (470 to 690 board feet.)

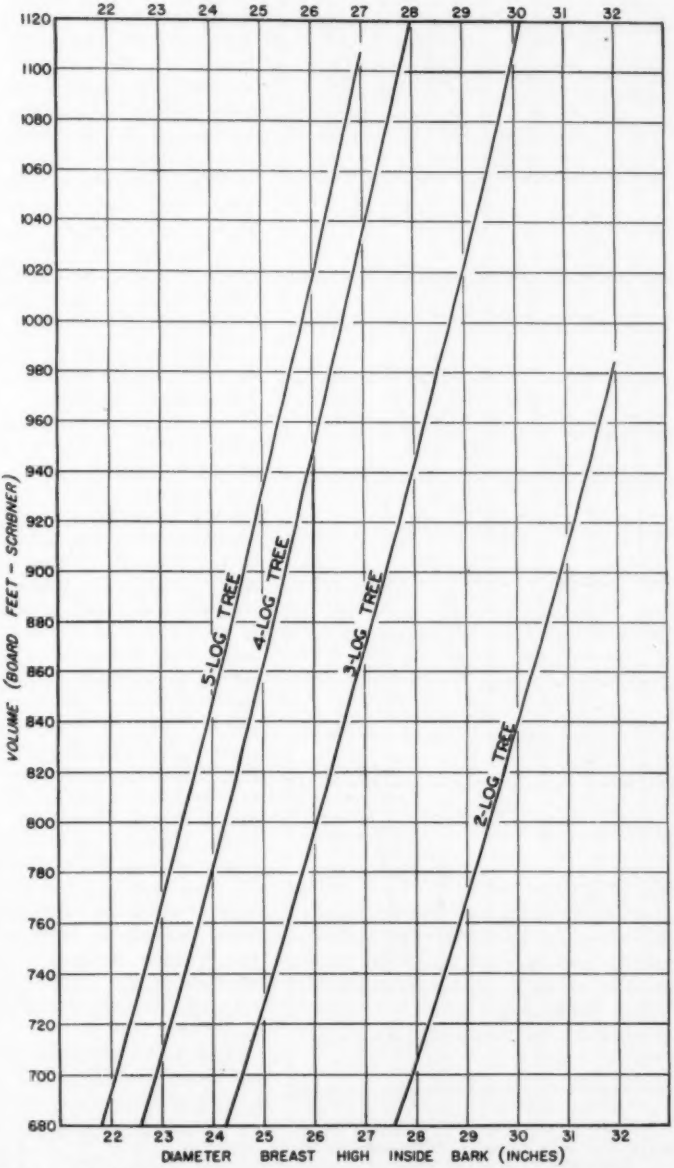


FIGURE 4.—Correlation of volume with diameter breast high inside bark. (680 to 1,120 board feet.)

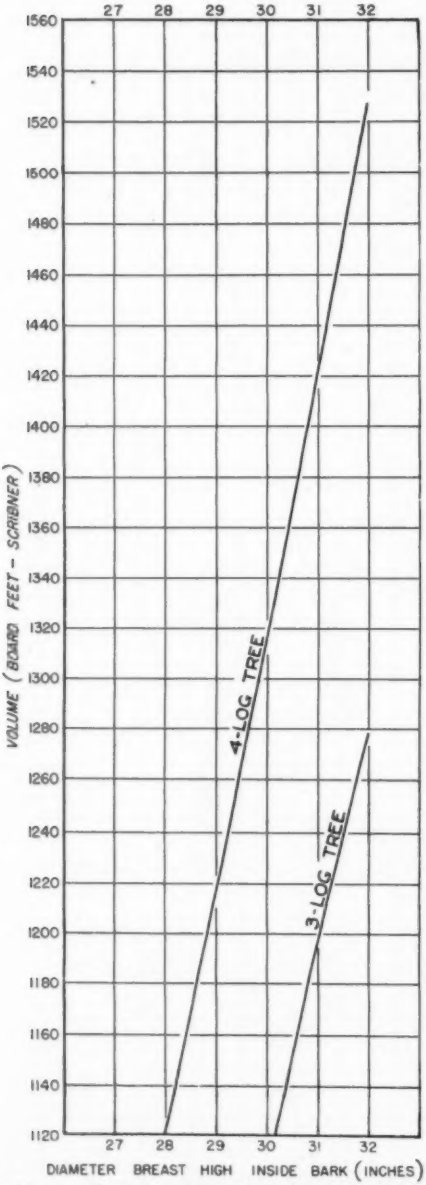


FIGURE 5.—Correlation of volume with diameter breast high inside bark. (1,120 to 1,560 board feet.)

Next, the volume of each sample tree was estimated from the curves, and this estimated volume was divided into the actual volume of the tree (determined from individual stem measurements). The quotients thus obtained were denoted as R. For trees with less butt swell and with better form than average, the R's are greater than 1.0; for trees of poor form and large degree of butt swell, the R's are less than 1.0.

These R's were then correlated with D and B. The trees were sorted into B classes, and a curve of R over D was drawn for each B class. Here again, the curves were parallel and in logical order, indicating the absence of joint relationships. A single curve (fig. 6) was, therefore, drawn to represent the net trend of R with D. The R was then estimated from this curve for each sample tree, and the differences were computed between these estimated R's and the actual R's. These residuals (termed r) were then plotted over B, and a curve fitted (fig. 7). From this curve a correction was read for each sample tree and applied to the value of R as estimated from the curve of R over D. These estimated and corrected R's were then compared with the actual R's.

The differences between the corrected R's and the actual R's were then sorted by log classes and subsorted by diameter classes. Next

the differences were converted into board feet and plotted against the original set of basic curves of volume over diameter breast high inside bark. These curves were then redrawn wherever it appeared necessary. New volumes were estimated from these curves, new R's computed, and these R's again correlated with the D and B factors just as in the first approximation. This process was repeated several times until no further adjustments in the fit of any of the curves were necessary. All of the curves were fitted freehand.

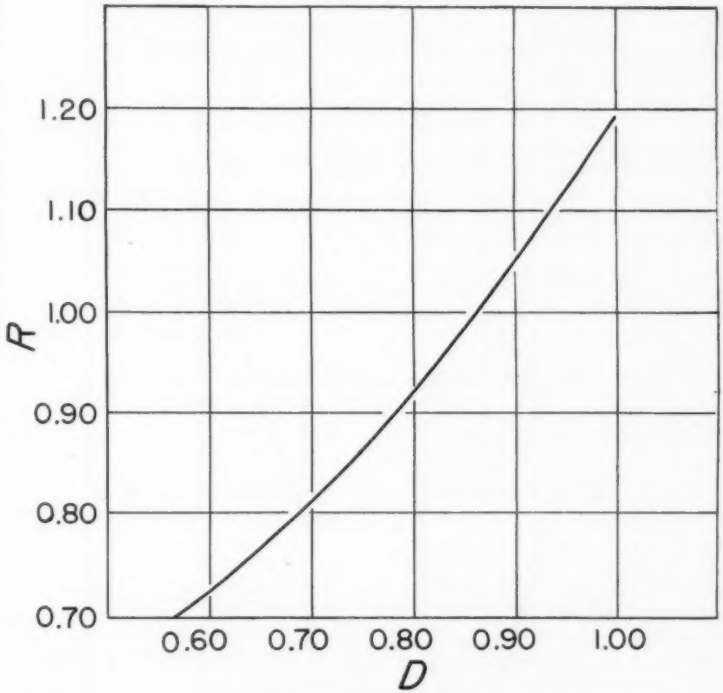


FIGURE 6.—Correlation of R with D.

When all the curves had been finally fitted, the differences between the actual R's and the estimated R's were sorted by species. If the factors used in constructing volume tables by this method are really effective in measuring the differences between species, the final average residual of one species should not be significantly different from that of another species, and they should all be close to zero. Table 3 shows the average residual of R for each of the species used in developing the method.

The average residuals of R shown in table 3 are numerically equivalent to the average deviations of estimated volume from actual volume expressed as a percent of the estimated volume.

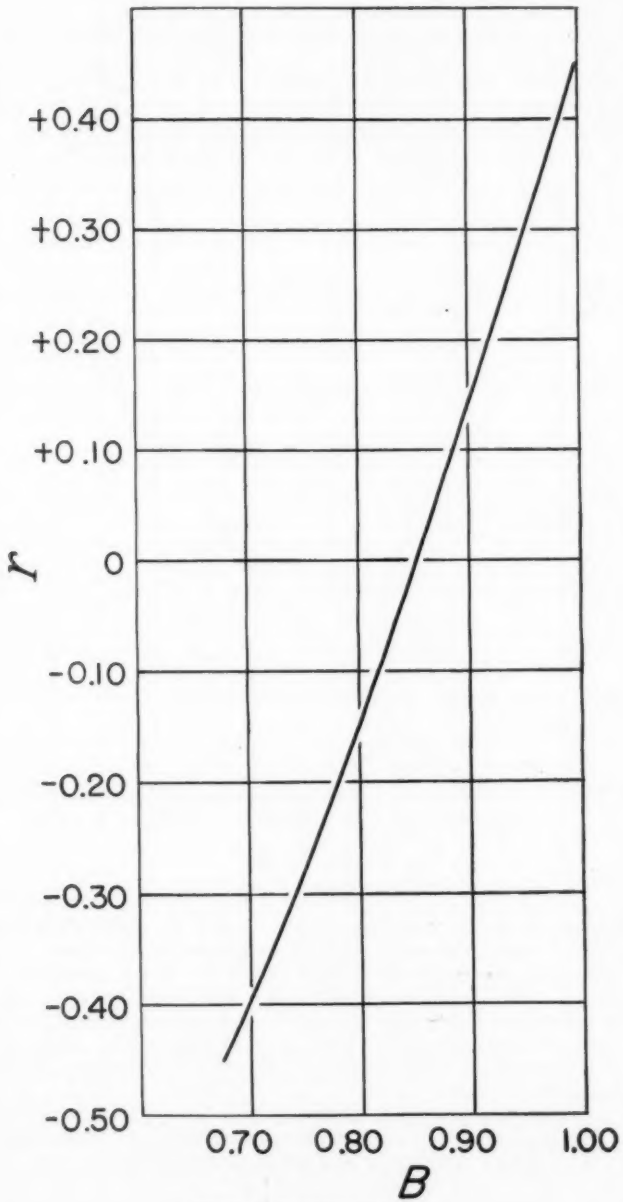


FIGURE 7.—Correlation of r with B.

TABLE 3.—*Average residuals by species*

Species	Trees	Average residual	Species	Trees	Average residual
	Number	*Percent*		*Number*	*Percent*
Sugar maple	166	+0.31	Jack pine	57	−1.12
Yellow birch	137	−.31	Norway pine (second growth)	117	−.50
Basswood	275	+.70	Norway pine (old growth)	183	+1.80
Hemlock	239	−.70			

Fisher's analysis of variance test[5] was used to determine the significance of the differences between the observed residuals. Although the test showed that the differences are significant, they are actually so small and so slightly removed from zero that the fact of statistical significance is of little practical importance. It should be noted (table 3) that the difference between the two groups of Norway pine is nearly as great as the difference between the most extreme cases (Norway pine old growth and jack pine). The residuals are chiefly the result of variations in volume associated with taper in the portion of the tree above two logs, over which portion the method affords no direct control.

As a test the volumes of several groups of trees which had not been used in developing the method were estimated and the residuals listed in table 4 were obtained.

TABLE 4.—*Average residuals of species not used in developing the method*

Species	Trees	Average residual	Species	Trees	Average residual
	Number	*Percent*		*Number*	*Percent*
Shortleaf and loblolly pines	165	−0.41	Sugar maple	210	−.20
Mixed southern hardwoods	79	−.95	White pine	80	+.69
Red gum	118	−.84			

The index of correlation is another measure of the effectiveness of the method. In order to test the theory of the method rather than its accuracy under field conditions, the volume of each sample tree was estimated, using its individual D and B factors, a method which is not practicable under field conditions. By working in this manner, a correlation index of 0.9765 was obtained. Thus it was demonstrated that a very large proportion (95 percent) of the variance in volume is accounted for by the variables taken into consideration.

APPLICATION OF THE METHOD

COLLECTION OF DATA

In collecting sample tree measurements to be used in constructing volume tables by this method, the objective should be to sample as well as possible the area to which the table is to be applied. The number of trees to be measured depends on the accuracy desired and the uniformity of the area. On the basis of this study it appears that 100 trees will generally give average values of D and B with standard errors of less than 0.005. For use in restricted areas, where greater

[5] FISHER, R. A. STATISTICAL METHODS FOR RESEARCH WORKERS. Ed. 4, 307 pp., illus. Edinburgh and London. 1932.

constancy of form and butt swell can be expected, a smaller number of trees will suffice.

Only four measurements are needed from each sample tree. These are (1) diameter breast high outside bark, (2) diameter breast high inside bark, (3) inside-bark diameter at 18.3 feet above the ground, and (4) inside-bark diameter at 34.6 feet above the ground. Only trees with a reasonably normal form should be measured; trees with pronounced irregularities at the points of measurement should be avoided. Even though such trees do occur in the area to which the volume table is to be applied, their inclusion among the sample trees only adds inaccuracy to the estimate of the normal trees.

COMPUTATION OF FORM AND BUTT SWELL FACTORS

After the measurements have been collected, the next step is to compute the values of the two factors, B and D, for each tree, using the following formulas:

$$B=\frac{\text{Diameter inside bark at 18.3 feet}}{\text{Diameter inside bark at breast height}}$$

$$D=\frac{\text{Diameter inside bark at 34.6 feet}}{\text{Diameter inside bark at 18.3 feet}}$$

After these two factors have been computed for each sample tree, either of two methods may be followed, depending upon the amount of data on hand and the accuracy desired. The first and simplest method is to determine the arithmetic average of each of the two factors by summing the individual values and dividing by the number of observations. The second method involves the correlation of B and D with diameter and height. This scheme is merely a modification of the first method and follows it analogously.

The following numerical example illustrates the computation. Measurements were first taken on 296 yellow birch trees in the Upper Peninsula of Michigan. From these data the average D was found to be 0.87 and the average B 0.84. The next step is to determine R from the curve shown in figure 6, or from the values in table 5.

TABLE 5.—*Values of R and D, as read from figure 6*

D	Value of R for hundredths indicated									
	0.00	0.01	0.02	0.03	0.04	0.05	0.06	0.07	0.08	0.09
0.60	0.73	0.73	0.74	0.75	0.76	0.77	0.77	0.78	0.79	0.80
.70	81	.82	.83	.84	.85	.86	.88	.89	.90	.91
.80	.92	.93	.95	.96	.97	.98	1.00	1.01	1.02	1.04
.90	1.05	1.06	1.08	1.09	1.11	1.12	1.14	1.15	1.16	1.18

From this table or the curve of figure 6 the R value which corresponds to a D of 0.87 is found to be 1.01.

The next step is to determine the correction factor to be applied to R; this factor is known as r and is found in figure 7 or table 6 by looking up the r which corresponds to the average value of B (0.84).

TABLE 6.—*Values of r and B as read from figure 7*

B	Values of *r* for hundredths indicated									
	0.00	0.01	0.02	0.03	0.04	0.05	0.06	0.07	0.08	0.09
0.60								−0.46	−0.44	−0.42
.70	−0.40	−0.38	−0.35	−0.33	−0.30	−0.28	−0.26	−.23	−.20	−.18
.80	−.15	−.12	−.10	−.07	−.04	−.01	+.02	+.05	+.08	+.11
.90	+.14	+.17	+.20	+.23	+.26	+.29	+.32	+.35	+.38	+.42

In this case *r* equals −0.04. This value is then applied (added or subtracted according to the sign given in the table) to the value of *R* already found, and the result, in this case 0.97 (1.01−0.04=0.97), is used to adjust the basic table of volume over diameter inside bark. These volumes are presented in figures 1 to 5 and also in tabular form in table 7.

TABLE 7.—*Volume in board feet, Scribner decimal C rule by diameter breast high, inside bark, and merchantable length in 16.3-foot logs*

Diameter breast inside bark (inches)	Volume by merchantable length in number of 16.3-foot logs				Diameter breast inside bark (inches)	Volume by merchantable length in number of 16.3-foot logs			
	2	3	4	5		2	3	4	5
	Board feet	*Board feet*	*Board feet*	*Board feet*		*Board feet*	*Board feet*	*Board feet*	*Board feet*
8	31	43			21	370	480	574	624
9	44	59			22	412	538	640	694
10	59	76	88		23	453	598	708	767
11	78	97	114		24	497	663	781	845
12	98	121	145	168	25	544	728	861	930
13	121	148	179	204	26	593	795	946	1,016
14	146	178	216	243	27	645	868	1,034	1,107
15	171	213	256	287	28	705	942	1,121	
16	198	249	301	334	29	768	1,021	1,217	
17	228	288	346	385	30	837	1,106	1,317	
18	260	330	398	438	31	908	1,197	1,421	
19	295	377	450	496	32	984	1,278	1,527	
20	332	426	509	559					

All that remains is to multiply the curved or tabular volumes by 0.97 and then convert to an outside-bark basis.[6]

PROCEDURE FOR ONE-LOG TREES

It will be noticed that there is no volume curve for one-log trees. Since the merchantable length of these does not extend to 34.6 feet it is not possible to compute the factor *D* for one-log trees. However, the product of the average value of the factor *B* and the inside-bark diameter at breast height of any tree is equal to the diameter inside bark at the top of the first 16.3-foot log of that tree, which, in the case of one-log trees, makes up the entire volume. Therefore, it is necessary only to look up the volume of a log of this diameter in table 8 to determine the volume of the tree. Using, for example, the average *B* found for yellow birch trees, 0.84, to find the volume of a tree

[6] In actual practice, time can be saved by reading from a curve of inside-bark diameter at breast height over outside-bark diameter at breast height the inside-bark diameters which correspond to whole inch values of outside-bark diameters, and then reading the volumes which correspond to these fractional values of inside-bark diameter from the curves.

with a diameter breast high inside bark of 14.8 inches (corresponding to an outside-bark diameter at breast height of 16 inches) it is necessary to multiply the diameter breast high by the factor (14.8×0.84). The result, 12.4 inches, is the diameter inside bark of the top of the first log. The volume of this log is found, in table 8, to be 93 board feet, which is then assigned as the volume of one-log trees with an outside-bark diameter breast high of 16 inches. This procedure is followed for all diameter classes. In order to avoid interpolation or curving, it is advisable to determine the inside-bark diameters at breast height which correspond to whole inch values of diameter breast high outside bark before computing the volumes.

TABLE 8.—*Scale of 16-foot logs read to nearest board foot from Scribner Decimal C rule computed by formula* $V=0.79D^2-2D-4$

Diameter inside bark (inches)	Volume for tenths of inch indicated									
	0.0	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9
	Bd. ft.	*Bd. ft.*	*Bd. ft.*	*Bd. ft.*	*Bd. ft.*	*Bd. ft.*	*Bd. ft.*	*Bd. ft.*	*Bd. ft.*	*Bd. ft.*
6	12	12	13	14	15	16	17	18	19	20
7	21	22	23	24	24	25	26	27	28	29
8	30	31	32	33	34	36	37	38	39	41
9	42	43	45	46	47	48	50	51	52	54
10	55	56	58	60	61	63	64	66	67	69
11	70	72	74	75	77	78	80	81	83	84
12	86	88	90	91	93	95	97	99	101	102
13	104	106	108	110	111	113	115	117	119	121
14	123	125	127	129	131	133	135	137	140	142
15	144	146	148	150	153	155	157	159	161	164
16	166	168	171	173	175	177	180	182	185	187
17	189	191	194	196	199	202	204	207	210	213
18	216	218	221	224	227	229	231	234	237	240
19	243	245	248	251	254	257	260	263	266	269
20	272	275	278	281	284	287	290	293	296	299
21	302	305	308	311	314	317	320	323	327	330
22	334	337	340	344	348	351	354	358	361	365
23	368	372	375	379	382	386	390	394	397	400
24	403	407	410	414	417	422	425	428	431	435
25	440	443	447	450	455	458	462	466	470	474
26	478	482	486	490	494	497	502	506	510	514
27	518	522	526	530	534	537	542	546	550	554
28	559									
29	602									

MODIFIED PROCEDURE

If very exact results are desired and there is sufficient material at hand, the values of D and B can be correlated with diameter breast high alone or with diameter breast high and height. In many cases the correlation is so slight that it can be ignored and the simple averages of D and B used. When a fair degree of correlation is found, however, the volume table can be improved by estimating D and B for each diameter class separately and determining the corresponding corrected R's. Once the curves of D and B have been established, this procedure is equally simple and direct.

A number of other modifications are possible and will suggest themselves to anyone working with the method.

APPLICATION OF THE TABLES IN THE FIELD

Much of the dissatisfaction with the older types of tables has its origin in the application of the tables in the field. When properly used they give excellent results, but it is necessary to follow exactly the specifications which were set up when the tables were constructed.

Tables of the type described here can be used with much greater flexibility and with little chance of mistakes in application. The tables present the volume in board feet (according to the Scribner decimal C rule computed by the formula $V=0.79D^2-2D-4$), above a 2-foot stump and up to whatever height the tree is merchantable regardless of diameter at that point, provided it is over 6 inches. The merchantable height should be estimated to the point where actual utilization will cease, which in most cases will be determined by the presence of large limbs or bole deformities. So long as the merchantable length is not carried up into the top where the main stem becomes rough and irregular, the table will give highly accurate results. Field checks have shown that the volumes given agree very closely with the actual volume removed in logging operations.

If there are species which have extremely low values of both D and B (below 0.65–0.78) the volumes as given by this method will be slightly low. Such low values, however, were not found in any of the species used in this study, and are unusual.

SUMMARY

A new and simple method of constructing board-foot volume tables is presented. This method takes into account the fact that the upper limit of merchantability is more often fixed by the position of large limbs or deformities than by minimum diameter. A set of basic curves of volume over diameter at breast height, inside bark, serves as the foundation. These curves are modified by the use of two numerical measures of form and butt swell so that they will fit any species coming within the size range of the material presented.

The construction of tables by this method presents several advantages not found in other methods. The collection of data is simplified because only a relatively few trees must be measured and only four measurements are required from each tree. In the computation of the field data only two simple ratios need to be worked out for each tree and an average of each computed. It is not necessary to determine the actual volume of the trees. There is the added advantage that only one result is possible—there is no chance for variation between tables made by several workers from the same data. Thus, no highly specialized knowledge is necessary for the construction of tables by this method.

Accuracy of the volumes computed from this type of table has been demonstrated by actual measurement of logs.

RHYNCHOSPORIUM SCALD OF BARLEY, RYE, AND OTHER GRASSES[1]

By RALPH M. CALDWELL

Associate pathologist, Division of Cereal Crops and Diseases, Bureau of Plant Industry, United States Department of Agriculture [2]

INTRODUCTION

Scald of barley, rye, and other grasses, caused by *Rhynchosporium* spp. is a common foliage disease in many parts of the world. In certain regions of North America it has been one of the principal limiting factors of barley production. Little study has been given this disease by pathologists in the United States and only slightly more in Europe. The present studies, initiated in Wisconsin in 1926, comprise a general consideration of the taxonomy, physiology, and host specialization of the causal fungus and of the host-parasite relationships, and seasonal development of the disease. The findings relative to physiologic specialization and pathological histology stand in marked contrast to those of Bartels (*1*) [3] in Germany and Brooks (*2*) in England. Two preliminary reports have been published on this work (*3*, *4*).

THE DISEASE

COMMON NAME

Several common names have been applied to the disease referred to as "scald" in this paper. These include "leaf blight", "leaf spot", "leaf blotch", and "scald." With the exception of the latter, each of these has been used to designate another cereal disease and is avoided here to prevent confusion. The term "scald", besides being distinctive among cereal disease names, has in its favor the facts that it is accurately descriptive of the disease in its most aggressive form and that recently it has been frequently used.

HISTORY, DISTRIBUTION, AND ECONOMIC IMPORTANCE

Oudemans (*17*) first recorded the discovery of the scald organism in June 1897, having found it on rye (*Secale cereale*) in the Netherlands. He reported it under the name *Marsonia secalis* n. sp. Frank (*11*), in October 1897, gave the first adequate description of the disease, reporting it on barley and rye in Germany. He recognized it to be of considerable economic importance on barley, particularly when the plants were attacked in advance of the heading stage. Seedling plants of barley were reported to be killed by severe attack. Frank's examination of herbarium specimens revealed the presence of the disease in Germany in 1894, which is its earliest known occurrence.

[1] Received for publication Apr. 13, 1937. Issued August 1937. Cooperative investigations by the Division of Cereal Crops and Diseases, Bureau of Plant Industry, U. S. Department of Agriculture, and the Departments of Plant Pathology and Botany of the University of Wisconsin, and the Department of Botany, Purdue Agricultural Experiment Station.

[2] The writer gratefully acknowledges the assistance of Drs. J. G. Dickson and E. M. Gilbert of the University of Wisconsin during the progress of these studies.

[3] Reference is made by number (italic) to Literature Cited, p. 198.

Frank reported inoculation experiments by E. Heinsen proving the relationship of the causal fungus. Heinsen (*12*), in 1901, published a full account of his experiments with scald, referred to by Frank. His inoculations showed barley and rye to be susceptible, wheat slightly susceptible, and oats immune.

Since these early papers scald has received little attention other than in records of occurrence and a report of resistance in barley by Johnson and Mackie (*13*), until the recent publications of Brooks (*2*), Bartels (*1*), and Mackie (*16*). The disease was first mentioned in American literature in 1917,[4] when it was reported to have been prevalent in 1915 in the United States. It is now known to occur widely in northern Europe and in the United States, and in Canada, New South Wales, Tunis, Argentina, and Peru. Reports of severe losses from scald have come only from the United States and Germany. The disease occurs very frequently in severe form on the winter barley crop of the Pacific Coast States and Idaho. The most destructive epidemics have been reported in the interior valleys of California where a positive correlation was noted between scald resistance and yield (*6*). Barley yields in this region have been estimated to be reduced as much as 20 to 30 percent (*5*). In the same State in 1925,[5] the disease was reported as "killing the leaves, shrivelling the kernels, and weakening the plants to such an extent that a reduction of yield of probably 25 percent occurred." Wiebe [6] makes the following report of barley scald in California, based upon comparative yields of susceptible and resistant varieties during epidemic and nonepidemic years: "In 1935 barley scald was a serious disease in California. Yields of susceptible varieties were reduced from 10 to 15 percent." Less frequently scald may become prevalent in other sections of the United States but has not been considered of major economic significance. In spring barley plots at Madison, Wis., in 1928, 1929, and 1930, the disease became abundant during the booting and heading stages of growth. The foliage was almost entirely killed, yet the plants matured and produced apparently normal heads and grain. Although yield reduction must have resulted, no measure of the loss could be made. In Europe, scald has been reported as severe on the seedling and mature plants by Frank (*11*) and Heinsen (*12*). Brooks (*2*) states that susceptible varieties in England, although suffering loss of almost all the lower leaves, recovered as the plants matured, and showed no appreciable effect of the disease at harvest time.

PLANTS ATTACKED

In addition to very commonly attacking barley (*Hordeum vulgare* L. and *H. distichum* L.) and rye (*Secale cereale* L.), scald has been reported twice on wheat (*Triticum aestivum* L., *T. vulgare* Vill.), once in Germany (*12*), and once in Washington State in the United States.[7] It was also once reported on oats (*Avena sativa* L.) in Denmark (*14*).

A number of grasses belonging to seven genera are also reported to be attacked. The literature to date lists the following occurrences of this disease on grasses, namely, *Agropyron repens* (L.) Beauv. in

[4] United States Bureau of Plant Industry. Disease caused by rhynchosporium graminicola. U. S. Bur. Plant Indus. Plant Disease Bull. 1: 9. 1917. [Mimeographed.]

[5] Haskell, R. J. Scald caused by rhynchosporium secalis (oud.) davis. U. S. Bur. Plant Indus. Plant Disease Reptr. Sup. 48: 341. 1926. [Mimeographed.]

[6] Personal correspondence with G. A. Wiebe, Division of Cereal Crops and Diseases, Bureau of Plant Industry, U. S. Department of Agriculture.

[7] Johnson, A. G., and Haskell, R. J. rhynchosporium graminicola . . . U. S. Bur. Plant Indus. Plant Disease Bull. Sup. 8: 37. 1920. [Mimeographed.]

Wisconsin (*3*, *8*), Oregon;[8] Denmark (*14*), and Germany (*1*); *A. dasystachyum* (Hook.) Scribn. in Oregon;[8] *Bromus inermis* Leyss. in Wisconsin (*3*, *9*); *B. mollis* L. in England (*2*); *B. sterilis* L. in England (*2*); *Dactylis glomerata* L. in Wisconsin (*9*), England (*2*), and Oregon;[8] *Danthonia* sp. Lam. and DC. in Oregon;[9] *Elymus robustus* Scribn. and J. G. Sm. (*canadensis*) in Wisconsin (*4*); *E. glaucus* Buckley in

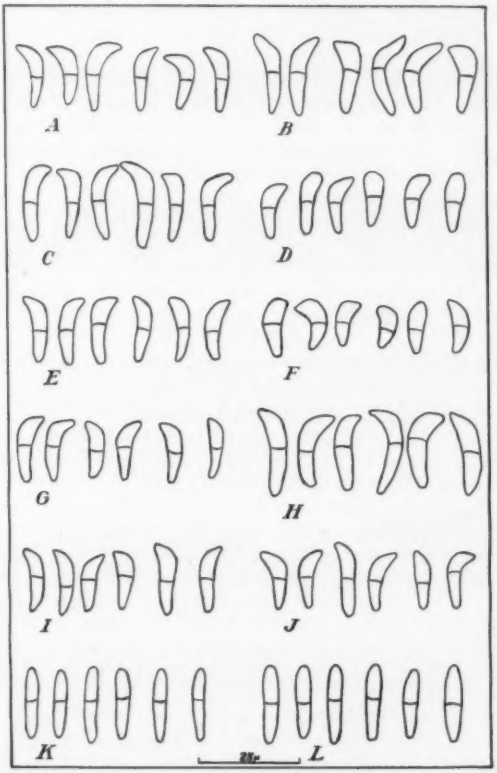


FIGURE 1.—Morphology of conidia of races of *Rhynchosporium secalis* and of *R. orthosporum*, produced on their respective hosts and in cultures isolated from these hosts. *A*, *B*, Barley race of *R. secalis* from host and culture respectively; *C*, *D*, rye race of *R. secalis* from host and culture respectively; *E*, *F*, *Agropyron repens* race of *R. secalis* from host and culture respectively; *G*, *H*, *Bromus inermis* race of *R. secalis* from host and culture respectively; *I*, *J*, *Elymus canadensis* race of *R. secalis* from host and culture respectively; *K*, *L*, *R. orthosporum* from host and culture respectively.

Oregon;[8] *Hordeum jubatum* L. in Wisconsin (*3*) and Oregon;[8] *H. murinum* L. in Germany (*1*) and Oregon;[8] *Lolium perenne* L. in Germany (*1*) and Oregon;[8] *L. multiflorum* Lam. in Oregon;[8] *Milium effusum* L. in Denmark (*14*). In addition, the writer has found the disease on *Elymus virginicus* L. in Indiana and on *Hordeum jubatum* L. in South Dakota.

Dactylis glomerata has been found by the writer in Wisconsin attacked by an undescribed species of *Rhynchosporium* differing from

[8] SPRAGUE, R. A PRELIMINARY CHECK LIST OF THE PARASITIC FUNGI ON CEREALS AND OTHER GRASSES IN OREGON. U. S. Bur. Plant Indus. Plant Disease Reptr. 19: [156]–186. 1935. [Mimeographed.]
[9] HASKELL, R. J. See footnote 5.

R. secalis in the cylindrical shape and lack of apical beak of the conidia (fig. 1, *K*, *L*). The symptoms of the disease are very similar to those caused by *R. secalis* on other hosts. An examination of the collection from which Drechsler (*9*) reported *R. secalis* on this host has shown the conidia to be those of this undescribed species. This species has also been collected by Sprague[8] in Oregon and submitted to the writer for identification. Thus, the only two reports of *Rhynchosporium* on *D. glomerata* in the United States have proved to be based on the new species rather than on *R. secalis*. The description of the new species, designated as *R. orthosporum* sp. nov., is given herein in the section on Taxonomy and Nomenclature.

A number of grass species not reported as naturally infected in the field have been infected by artificial inoculation with *Rhynchosporium secalis*. Bartels (*1*) reports the following species artificially infected with inoculum collected in Germany: *Lolium italicum*, *Poa pratensis*, *P. nemoralis*, *P. compressa*, *P. trivialis*, *Bromus arcensis*, *Agrostis stolonifer*, *Cynosurus cristatus*, *Phleum pratense*, and *Holcus lanatus*. The writer has artificially infected the following species, unknown to be naturally infected: *Agropyron tenerum*, *Bromus arenarius*, *B. lanuginosus*, *B. madritensis*, *B. villosus*, *Elymus striatus*, *Hordeum nodosum*, and *H. pusillum*.

SYMPTOMS

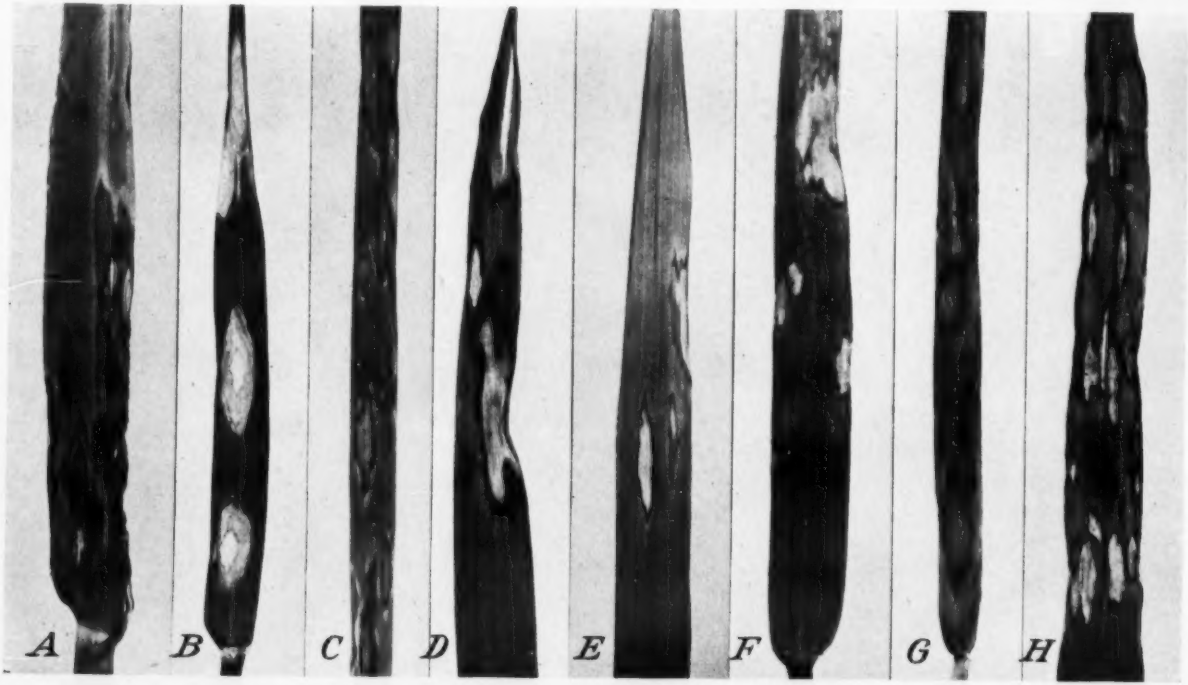
Scald as it occurs in Wisconsin, and as it has been described most frequently, is primarily a foliage disease attacking most conspicuously the blades, and to a lesser degree the leaf sheaths. The disease symptoms are strikingly similar upon all of the hosts observed by the writer (pl. 1) and may easily be recognized and distinguished from those of other leaf-spotting diseases of cereals and grasses. In the early stages of development, the lesions are of a dark bluish-gray color with a water-soaked appearance. Such areas are often 1 to 2 cm in length before evident collapse of the tissue occurs. This collapse takes place very rapidly, and in this stage, especially upon barley where large numbers of lesions are coalescing, the impression of rapid scalding is created. Lesions developing separately tend to assume a lenticular shape. The scalded area soon dries and the center assumes a light-gray color. The margin assumes a dark-brown color, which is the most distinguishing feature of the scald leaf spot. Successive enlargements of the lesions may occur and concentric brown rings result (pl. 1, *A*, *B*), giving the lesion a zonate appearance. Leaves are completely destroyed by severe infection and often almost complete defoliation of the host results.

PATHOLOGICAL HISTOLOGY

The relation of the scald fungus to the host tissue and the development of the disease have been studied microscopically upon barley leaves naturally infected in the field and artificially infected in the greenhouse. Stages in the development of the disease from penetration of the host to complete break-down of the leaf tissue and fructification of the pathogene have been followed.

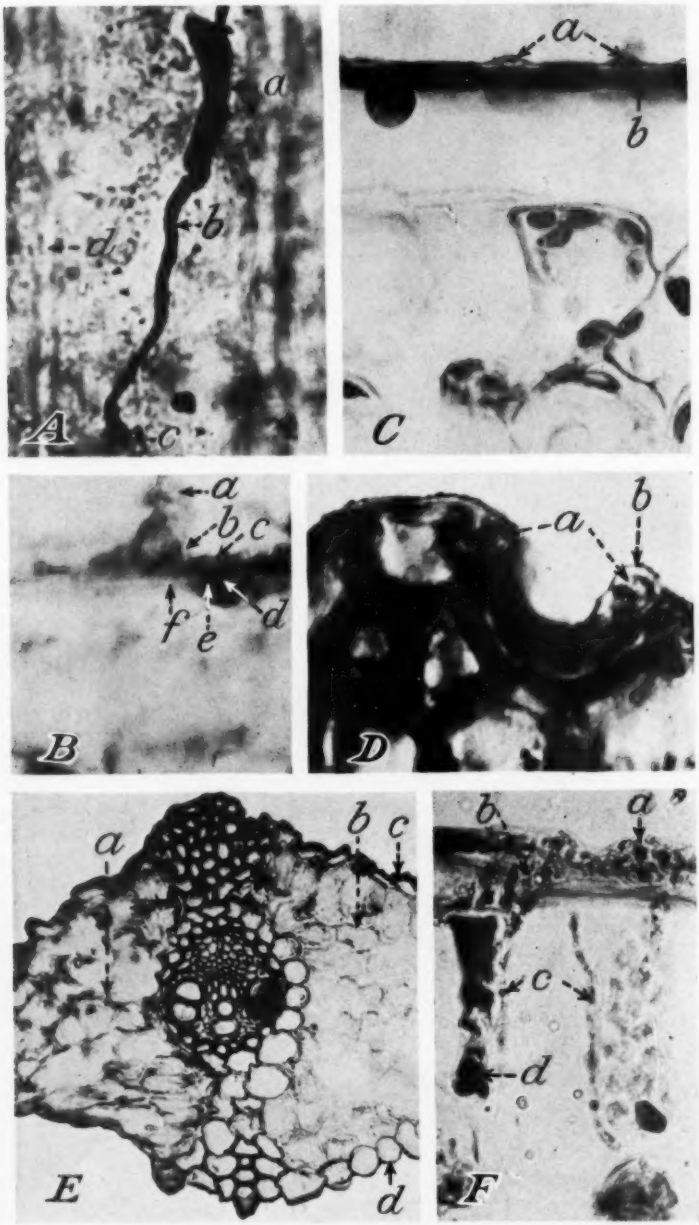
In the study use was made of both longitudinal and transverse sections of the leaf and of cleared whole leaf segments. Material for sectioning was fixed in both chrom-acetic urea and formalin-acetic-alcohol fixa-

[8] See footnote on page 177.



SYMPTOMS OF SCALD ON CEREALS AND GRASSES IN THE FIELD.

A, Barley; *B*, rye; *C*, *Bromus inermis*; *D*, *Elymus canadensis*; *E*, *Elymus virginicus*; *F*, *Agropyron repens*; *G*, *Hordeum jubatum*; *H*, *Dactylis glomerata*. *A* to *E*, natural size. *F* to *H*, × 1.5.



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tives, the former being the more satisfactory. Longitudinal sections 10μ in thickness and transverse sections 20μ in thickness proved satisfactory for study. Staining in safranin followed by fast green was the

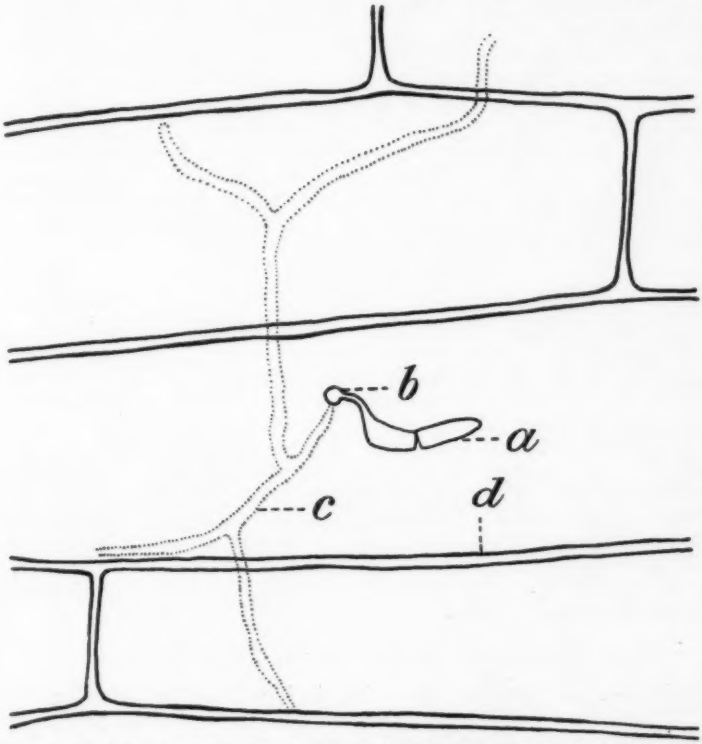


FIGURE 2.—Penetration of cuticle by *Rhynchosporium secalis* and development of subcuticular mycelium: *a*, Conidium; *b*, appressorium; *c*, subcuticular mycelium, *d*, vertical epidermal cell wall. Drawn with the aid of the camera lucida. × 700.

most useful technique used for differentiation of host and parasite tissues and pathological conditions in the host. The stages during conidium germination, appressorium formation, and after penetration

EXPLANATORY LEGEND FOR PLATE 2

A. Germinated conidium of *Rhynchosporium secalis* on a barley leaf. × 1,200. *a*, Conidium; *b*, germ tube; *c*, appressorium; *d*, vertical wall of epidermal cell.

B. Longitudinal section of seedling barley leaf showing penetration to the subcuticular position. × 1,900. *a*, Upper cell of conidium; *b*, short germ tube; *c*, appressorium; *d*, penetrating hypha; *e*, papillate growth on epidermal wall about point of fungus penetration; *f*, normal wall penciled to show clearly the normal thickness.

C. Longitudinal section of a young infection of a leaf of a nearly mature barley plant. × 1,440. *a*, Cross section of minute, slightly flattened, subcuticular hyphae; *b*, altered section of upper epidermal cell wall failing to retain safranin stain.

D. Transverse section of a collapsing lesion on a leaf of a nearly mature barley plant. × 1,800. *a*, Cross sections of subcuticular hyphae; *b*, cuticle of cell wall.

E. Transverse section of an advanced lesion on a leaf of a nearly mature barley plant. × 475. *a*, Collapsed mesophyll; *b*, normal mesophyll at margin of lesion; *c*, shows marginal advance of collapsing epidermis on dorsal surface over normal mesophyll at *b*; *d*, normal epidermis on ventral, noninfected side of leaf.

F. Longitudinal section of an advanced lesion on a leaf of a nearly mature barley plant showing penetration from the superficial stroma into the mesophyll. *a*, Superficial stroma; *b*, hyphae penetrating epidermal cell or cell wall; *c*, hyphae invading mesophyll; *d*, collapsing mesophyll cell adjacent to invading hyphae.

of the cuticle were satisfactorily studied in segments of whole leaves killed and partially cleared in a 50–50 mixture of 95-percent alcohol and glacial acetic acid, and stained in an aqueous solution of cotton blue. The conidia and germ tubes were heavily stained while the host tissue remained clear. Although the subcuticular hyphae could not be stained because of the covering of cuticle, they were clearly visible by microscopic observation, owing to light refraction.

Less complete observations of pathological histology have been made on scald of rye, *Agropyron repens*, and *Dactylis glomerata*. The macroscopic symptoms as well as internal pathology appear to be identical for scald on these hosts and on barley. Because of this similarity the scald of barley has been selected for study as a representative of the group of scald diseases, and all statements following refer specifically to scald of barley. All evidence at hand indicates that they apply also to the disease on the other hosts.

Mode of Infection

In the early stages of the development of *Rhynchosporium* in the host tissue the mycelium is wholly subcuticular. Penetration to the subcuticular position is effected within a 48-hour period. The germ tubes form very small rounded structures at the ends, apparently functioning as appressoria, from which penetration occurs (fig. 2 and pl. 2, *B*). Several appressoria may develop upon the branched germ tube system originating from a single conidium. Immediately beneath the appressoria the outer epidermal wall thickens to form a rounded papilla, several times the thickness of the wall, which projects into the lumen of the cell (pl. 2, *B*, *e*). The penetrating hypha grows into this thickening and then laterally in a subcuticular position (pl. 2, *B*, *d*, and fig. 2). Penetration may occur on either the dorsal or ventral epidermal surface.

Development of Fungus in the Host Tissue

Following penetration, the subcuticular mycelium grows rapidly and branches profusely. The first hyphae are very small in diameter and slightly flattened and oval in cross section (pl. 2, *C*, *a*). They remain very small for several days following infection. The average small diameter is about 0.6μ, while the large diameter averages about 2.2μ. After occupying a considerable area of the epidermal surface, the subcuticular hyphae enlarge (pl. 2, *D*, *a*) and impart a grayish cast to the infected area in contrast to the bright green of the surrounding tissue. The outer epidermal wall, which normally takes the safranin stain heavily, loses its affinity for this dye in the area immediately below the subcuticular hyphae (pl. 2, *C*, *b*) and becomes

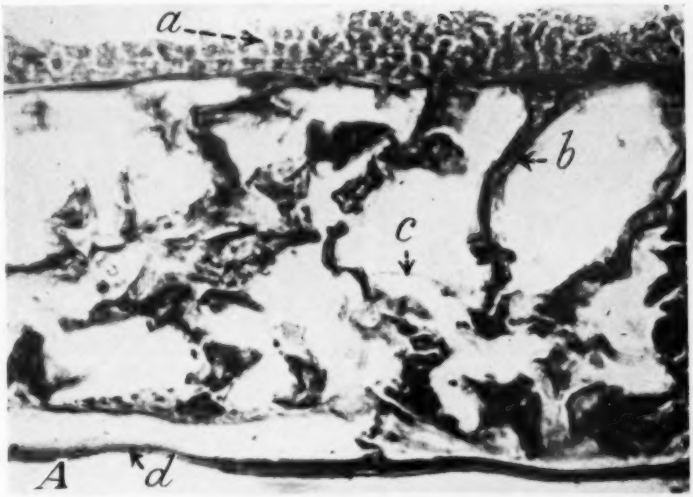
EXPLANATORY LEGEND FOR PLATE 3

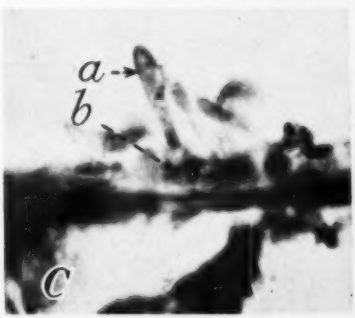
A. Longitudinal section of a mature lesion on leaf of a nearly mature barley plant, showing restriction of fertile stroma to one surface of the leaf. × 700. *a*, Fertile stroma; *b*, collapsed mesophyll cell; *c*, one of the rather few hyphae occurring within the mesophyll; *d*, noncollapsed epidermal cell on surface opposite the side of infection, no stroma occurring on this surface.

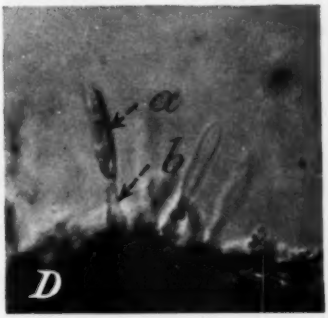
B. Longitudinal section of a mature lesion showing fertile stroma covering guard and epidermal cells. × 880. *a*, Superficial stroma; *b*, hyphae penetrating through macerated epidermal cell walls into mesophyll.

C. Longitudinal section of a mature lesion on barley, showing the distinctive manner of conidium production in *Rhynchosporium secalis*. × 1,300. *a*, Immature conidium, oriented to obscure the beaked, apical cell; *b*, cell of fertile stroma on which conidium is borne.

D. Free hand section of a lesion produced by *Rhynchosporium alismatis* (Oud.) Davis on *Alisma plantago-aquatica*, showing manner of sporulation. × 1,300. *a*, Immature nonseptate conidium (dark bands on conidium are not cross walls but stained cytoplasm, cross walls when present showing as white lines); *b*, flask-shaped conidiophore.







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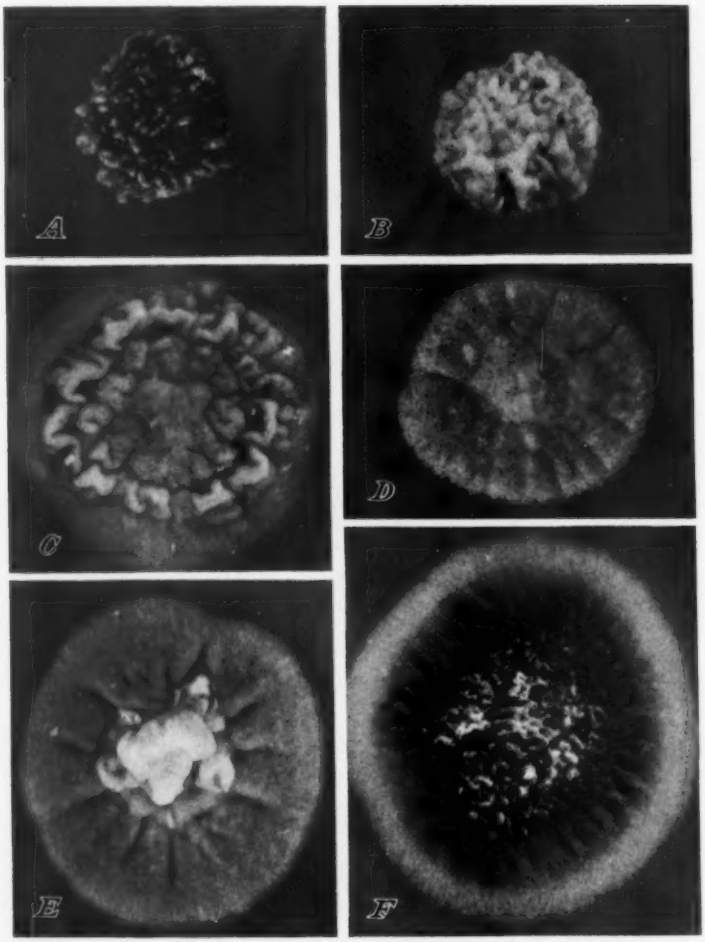

Photographs of 28-day-old culture of five physiologic races of *Rhynchosporium secalis* and one culture of *R. orthosporum* growing on potato 2 percent dextrose agar. × 1.75. *A*, Barley race of *R. secalis*; *B*, *Agropyron repens* race of *R. secalis*; *C*, *Elymus canadensis* race of *R. secalis*; *D*, rye race of *R. secalis*; *E*, *Bromus inermis* race of *R. secalis*; *F*, *R. orthosporum*

weakened as evidenced by frequent bending and sinking at such points. The outer epidermal wall is the first tissue to collapse, falling against the lower wall of the epidermal cell (pl. 2, *D* and *E*, *c*). Following the collapse of the epidermis, the mycelium begins to penetrate through the macerated walls of the collapsed epidermal cells into the mesophyll from the stroma which has been formed from the subcuticular hyphae (pl. 2, *F*, *b*, *c*, and pl. 3, *B*, *b*). Growth within the mesophyll is intercellular. Prior to this stage the mesophyll cells appear normal but rapidly collapse in the region of the invading mycelium (pl. 2, *F*, *d*, and pl. 3, *A*, *b*). At this stage the macroscopic symptom of scalding and water-soaking becomes evident in the leaf spots. Even after complete break-down of the mesophyll the mycelium makes only a sparse development in the interior of the leaf (pl. 3, *A*, *c*). This stage is reached about 9 days after inoculation in barley and after about 14 days in rye and the grasses under greenhouse conditions.

The infected area continues to enlarge by the radial growth of the subcuticular hyphae at its margin, the epidermis first collapsing, followed by successive penetrations of the fungus into the mesophyll (pl. 2, *E*, *c*). There is no evidence that radial growth of the intercellular mycelium within the mesophyll plays any important role as a means of enlarging the diseased area, since the subcuticular development of mycelium and subsequent epidermal collapse always considerably precede the appearance of hyphae in the underlying mesophyll at the margin of the lesion.

Fructification of the Fungus

During the invasion and break-down of the mesophyll, the subcuticular mycelium develops rapidly, covering the entire area of the leaf spot and building up a fertile stroma which may be several cells in thickness (pl. 3, *A*, *a*, and *B*, *a*). At this stage the cuticle has been pushed away from the wall and lost, leaving the stroma completely superficial. The greatest growth of the fungus is in this subcuticular and later superficial position, the mass of the fungus there far exceeding that within the mesophyll tissue. Fructification occurs after the complete break-down of the leaf tissue in the infected spot. The conidia are formed as direct outgrowths of the cells of the superficial, fertile stroma (pl. 3, *C*, *a*, *b*). Sporulation is most abundant in the central and most completely collapsed area of the leaf spot.

Owing to the restriction of the initial development of infection and subcuticular mycelium to one surface of the leaf, the fruiting stroma and sporulation are limited to that surface, although either surface may become infected (pl. 2, *E*, *c*, *d*, and pl. 3, *A*, *a*, *d*). The fungus does not grow through the leaf to fruit on the opposite surface. The fructifying surface can be identified macroscopically by the darker color of the leaf spot margin there, as contrasted with that on the opposite side. Fructification on both surfaces of a given leaf area occurs only where two separate infections take place on exactly opposite sides of the leaf.

Discussion of Pathological Histology

Penetration has been reported and figured by Bartels (*1*) as being effected primarily by the growth of conidial germ tubes through the stomata, directly into the mesophyll of the leaf. He also reported direct epidermal penetration as occurring less frequently. Mackie

(*16*) implied stomatal entry by stating that the germ tubes "form appressoria in the stomata." The observation of hundreds of germinating conidia and penetrations, in this study, has given no evidence of even the rare occurrence of stomatal entry. Germ tubes repeatedly have been observed to have grown across the surfaces of stomata to form appressoria on the upper epidermal wall elsewhere. The early stages of the pathology of the scald disease, involving abundant subcuticular development of mycelium prior to its appearance within the mesophyll tissue, precludes the possibility of stomatal entry being of significance in the initiation of infection.

Bartels (*1*) has figured the fungus as first developing within the mesophyll and later growing out to the epidermis to form the fertile mycelium within the lumen of epidermal cells of both the dorsal and ventral surfaces. Brooks (*2*), while not following penetration of the fungus, gives an account of fructification similar to that of Bartels, assuming preliminary entry of the mycelium into the mesophyll and later growth out to a subcuticular position or into the lumen of the epidermal cells where fructification occurs. Failing to understand the manner of the initiation of parasitism of *Rhynchosporium*, these workers have apparently interpreted the penetration from the subcuticular mycelium into the mesophyll as occurring in the reverse order. The writer has never observed a case where the fruiting stroma developed initially within the lumen of the epidermal cells. Occasionally, as shown in plate 2, *F*, *b*, hyphae penetrating into the mesophyll appear to have traversed the lumen of the epidermal cells. A more likely interpretation, however, is that they have grown down through the vertical wall of the epidermal cells, which are indiscernible, as is most wall tissue in the presence of masses of the fungus. It is possible that, after break-down of the epidermal cells, the fertile mycelium may develop within the macerated walls of these cells. It is certain, however, that in the writer's material, hyphae did not enter the lumen of epidermal cells preliminary to formation of the fruiting stroma.

Davis (*8*) stated that the conidia are borne on undifferentiated hyphae protruding from stomata. The papers of Frank (*11*) and Brooks (*2*) and the present work concur in showing this to be incorrect.

THE CAUSAL ORGANISM

TAXONOMY AND NOMENCLATURE

The Genus Rhynchosporium

The taxonomy and nomenclature of the genus *Rhynchosporium* have become confused in European and American literature. The first mention of the genus *Rhynchosporium* occurs in a publication by Frank (*11*) in October 1897, in which the author credits the naming of the new genus to his associate, E. Heinsen, who had not yet published his work. Heinsen (*12*) in 1901 published on this work. Both Frank and Heinsen failed to give formal descriptions of the genus or species, merely giving a general description of the fungus with illustrations. Formal descriptions were later provided by Saccardo (*18*) and Lindau (*15*), who credited authority for the genus *Rhynchosporium* and the species *R. graminicola* to Heinsen.

Davis (*8*) in 1922 emended the genus to include all Mucedinaceae, Micronemeae, Hyalodidymae. Davis conceived the conidia to be

borne in the following manner: "An undifferentiated hypha makes its way to a stoma where it bears upon its extremity a conidium." This statement has been shown to be in error by the present work and that of Brooks (*2*).

The taxonomic position of the genus *Rhynchosporium* is somewhat debatable since the genus appears to possess characters common to both the orders, Moniliales and Melanconiales. The apparent resemblance to the Melanconiales lies in the fructification from a stroma-like stratum. This stratum constitutes the main mycelial body of *Rhynchosporium*, being almost continuous over the affected portion of the leaf and more or less unlimited in its growth at its margin. The position of the stroma is essentially superficial on the leaf, although the initial growth of hyphae immediately following infection and at the margin of the stroma is in the subcuticular position. By proliferation of this mycelium the stroma is progressively built up from the center toward the margin of the leaf spot. The margin of the stroma grades into a diffuse nonstromatic mycelium, in a subcuticular position. The cuticle is soon pushed away and dislodged as the fruiting stroma is built up. Conidia are never produced within the host tissue, or even under the cuticle, later to be discharged.

In the existing keys to the genera, it is true that *Rhynchosporium* might conveniently be placed in the order Melanconiales or even considered synonymous with *Marssonina*. However, this study is interpreted as giving little evidence that *Rhynchosporium* is closely related to genera of this order. If such an interpretation were made, the whole more or less diffuse and superficial fungus body, which is often over 1 inch long and one-half inch wide, must be considered a single acervulus. Therefore, as the preferable alternative, the fruiting structure is here interpreted as a more or less compact, yet little organized mycelium, from which conidia are directly abstricted as in many other genera of the Moniliales. On the basis of these considerations *Rhynchosporium* is here recognized as a valid genus in the family Moniliaceae.

Frank's illustrations indicate that he correctly understood the morphology of the fruiting structures of the genus. However, the descriptions by Saccardo and Lindau are based on Heinsen's studies of the morphology of the fungus in culture and are misleading as to the morphology of the fructifying structure on the host, which, in the writer's opinion, is the important distinguishing feature of the genus. It seems necessary, therefore, to present here an emended description of the genus, including the characteristic features of fructification.

Rhynchosporium Heinsen.

Parasitic, producing spots on leaves; sterile mycelium sparse in mesophyll of host; mycelium subcuticular at first, later developing into a superficial fertile stroma more or less covering the leaf spot; conidiophores absent; conidia one-septate, hyaline, sessile on cells of fertile stroma.

The emended genus, *Rhynchosporium*, would fall in the classification, Moniliaceae, Hyalodidymae, Micronemeae.

Nomenclature of Rhynchosporium secalis (Oud.) Davis

The first published record of the scald fungus was made by Oudemans (*17*) in June 1897, under the binomial *Marsonia secalis*, 4 months previous to Frank's publication (*11*) on the same organism under the name *Rhynchosporium graminicola* Heinsen. Davis (*7*), in 1919, believing that Oudemans had incorrectly classified the fungus in the

Melanconiales, recognized Heinsen's genus *Rhynchosporium* in making the new combination *Rhynchosporium secalis* (Oud.) Davis.

Bartels (*1*), in 1928, made the combination *Marssonina graminicola* (Ell. and Ev.) Sacc., placing *Gloeosporium graminicolum* Ell. and Ev., *M. secalis* Oud., and *Rhynchosporium graminicola* Frank in synonymy. He recognized as having priority a description by Ellis and Everhart (*10, p. 154*) of *G.* (*Marsonia*) *graminicolum*, collected upon an unidentified grass by John Dearness at London, Canada. The description given of *G. graminicolum* has nothing in common with the characters of the scald fungus. Through the efforts of J. J. Davis, cotype material of *G. graminicolum* Ell. and Ev. has been secured from Dearness for study by the writer. This specimen is not the scald fungus and shows no similarity to it either in disease symptoms or fungus structure, and therefore can have no priority in the nomenclature. Ellis and Everhart's report (*10*) is accurately descriptive of the specimen. The internal morphology of the host strongly suggests it to be one of the Cyperaceae.

In view of the priority of Oudemans' description, the valid name of this species, then, is *Rhynchosporium secalis* (Oud.) Davis.

New Species

A new species of the genus *Rhynchosporium* has been collected in Wisconsin by the writer (*4*) and by Sprague [10] in Oregon, attacking *Dactylis glomerata*. This fungus produces symptoms identical with those of *R. secalis*. The fruiting structure is likewise similar. The new species, here designated as *R. orthosporum*, has uniformly cylindrical conidia which distinguish it from *R. secalis* (fig. 1). It is described below.

Rhynchosporium orthosporum sp. nov.

In foliis; maculis amphigenis, 0.5–3.0 cm longis, lenticularibus et saepe confluentibus, initio humido-fusco-olivaceis, margine concolori, dein centro canis, brunneo-marginatis; conidiis 14.4–19.4 × 2.3–4.7 μ, erectis, clyindraceis, medio 1-septatis, in stromatibus superficialibus sine basidiis et plus minusve maculas omnino occupantibus.

Hab. in foliis *Dactylidis glomeratae* in Wisconsin, 1929.

Rhynchosporium orthosporum sp. nov.

On leaves; spots, 0.5–3.0 cm long, lenticular in shape, coalescing to form irregular lesions, at first water-soaked, dark olivaceous, later becoming gray surrounded by a brown margin; conidia 14.4–19.4 × 2.3–4.7 μ, erect, cylindrical, medianly septate, formed directly on cells of superficial stroma, more or less covering leaf spot.

On *Dactylis glomerata* L., Whitewater, Wis., May 11, 1929, Caldwell (type); also from other locations in Wisconsin and from Benton County, Oreg.

Cotype specimens have been deposited in the herbarium of the University of Wisconsin and in the mycological collections of the Bureau of Plant Industry, United States Department of Agriculture.

Excluded Species

Davis (*8*) has made the combination *Rhynchosporium alismatis* (Oud.) Davis, placing *Septoria alismatis* Oud., *Aschochyta alismatis* Ell. and Ev., *Ramularia alismatis* Fautr., and *Didymaria aquatica* Starb., occurring on *Alisma* and *Sagittaria*, in synonymy with it.

[10] Sprague, R. See footnote 8.

Through the kindness of Dr. Davis, a fresh specimen of *Rhynchosporium alismatis* (Oud.) Davis on *Alisma plantago-aquatica*, collected by him at Klevensville, Wis., on July 12, 1929, was made available for study. Freehand and paraffin sections of this specimen show this fungus to lack the superficial fertile stroma and to bear the conidia on short flask-shaped conidiophores on the leaf surface (pl. 3, *D*). Thus, this species does not fall in the division Micronemeae as stated by Davis (*8*). The presence of conidiophores together with the lack of the superficial stroma excludes this species from the genus *Rhynchosporium*.

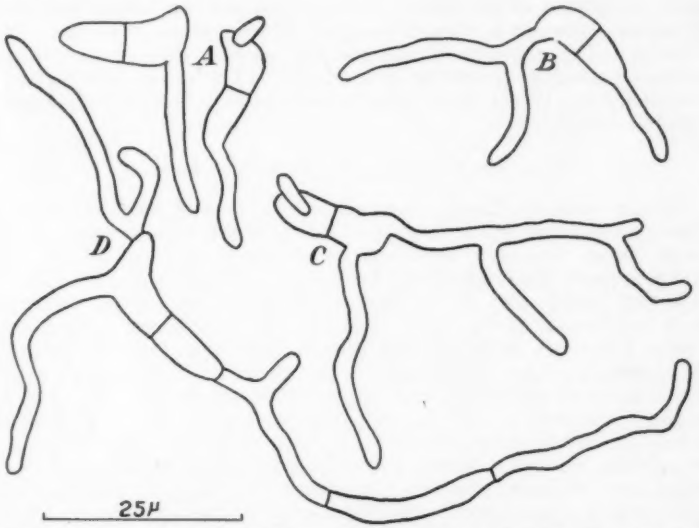

FIGURE 3.—Germination in water of culture-grown conidia of barley race of *Rhynchosporium secalis*: *A* to *D* represent growth stages after 8, 12, 24, and 36 hours, respectively.

Thus the genus as here defined includes only the species *Rhynchosporium secalis* (Oud.) Davis and *R. orthosporum* sp. nov.

ISOLATION AND CULTURE

Cultures of the scald organism from the several hosts may usually be obtained by the planting of small pieces of diseased leaf tissue on potato-dextrose agar after surface sterilization. Surface sterilization was accomplished by dipping the leaf pieces into 70-percent alcohol for 20 seconds, removing them to 1 to 1,000 mercuric bichloride solution for 1 to 2 minutes, and transferring them to agar plates after washing in sterile water. The fungus grows very slowly and requires 4 or 5 days to become macroscopically evident. Isolation during the warm summer months at Madison, Wis., is often difficult since the lesions are frequently overrun by various other fungi, predominantly *Alternaria* spp., which completely suppress the development of *Rhynchosporium*. When conidia from the host are available, cultures may be secured by pouring suspensions of conidia in

sterile water over agar plates and draining off the excess moisture. Isolated germinating spores usually must be located under the microscope and removed to agar slants soon after germination to avoid contamination.

The conidia of *Rhynchosporium secalis* and of *R. orthosporum* germinate upon agar within a 24-hour period. The details of the process, in the case of *R. secalis*, have been well described by Heinsen (*12*). The upper cell usually germinates first, with the germ tube swelling from the side of the cell or tip of the beak. The lower cell may then send out a tube. Either or both cells commonly produce a second tube after elongation of the first. Conidia germinating in distilled water are shown in figure 3. In water at 20° C., germination begins within 4 hours. The contents of the conidia, at first quite homogeneous, become vacuolate preceding germination. On agar, germination is initiated more tardily and germ tubes elongate more slowly than in distilled water.

Growth Response upon Different Media

All the races of *Rhynchosporium secalis* as well as the species *R. orthosporum* grow slowly in culture. The most rapid growth, on the media used, occurred upon potato-dextrose agar. The rye and barley races of the fungus have been cultured upon a variety of media including barley and rye-leaf-decoction agars, corn meal, and corn meal 1-percent dextrose agars, lima bean agar, oatmeal agar, potato, potato 1-percent dextrose, and potato 2-percent dextrose agars, 1- and 2-percent malt extract agars, and upon sterilized barley stems. The volume of mycelium and spores produced, within this range of media, apparently varied directly with the concentration of dextrose or soluble carbohydrate present. Judging from the conformation of the conidia, the most nearly normal development occurred on those media with low sugar content, i. e., corn meal, oatmeal, and lima bean agars, where conidia not unlike those from the host were produced (fig. 1). Conidia from potato dextrose and malt agars were of variable shape and appeared to be little more than undifferentiated terminal or branch cells of the fertile hyphae.

TEMPERATURE AND HUMIDITY RELATIONS

Conidial Germination and Germ-Tube Growth

To improve the inoculation technique, an experiment was conducted to determine the relation of temperature to spore germination and germ-tube elongation. Conidia of a culture isolated from barley were washed into sterile distilled water from 7-day-old corn meal-agar slant cultures. Drops of the spore suspension were transferred by a platinum loop to carefully cleaned cover glasses and were inverted as hanging drops over unsealed glass rings in Petri dishes. The bottoms of the Petri dishes were moistened with water. A selected standard-size loop was used to transfer all drops, giving them a uniform size. The hanging-drop, conidial suspensions were then incubated at temperatures ranging from 2° to 35° C. At certain intervals of time 25 spores were selected at random near the periphery of the drop and the longest germ tube of each spore was measured. Observations were continued for 48 hours. However, after 36 hours

branching of the germ tubes had become so profuse as to make measurements of germ-tube length unreliable as an index of growth. Only the germ tubes of conidia near the periphery of the drops were observed, since germination was more vigorous there. The data from this experiment are presented in figure 4. These curves show the minimum temperature for germ-tube growth in distilled water to lie between 2° and 4°, the optimum between 18° and 21°, with the maximum between 28° and 30°. The sudden reduction in rate of growth between 21° and 24° is striking. Similar reactions were evident in a number of germination trials where no measurements were made. The same temperature relation was observed in the case of the conidia from a culture isolated from rye but a more tardy germination occurred at all temperatures.

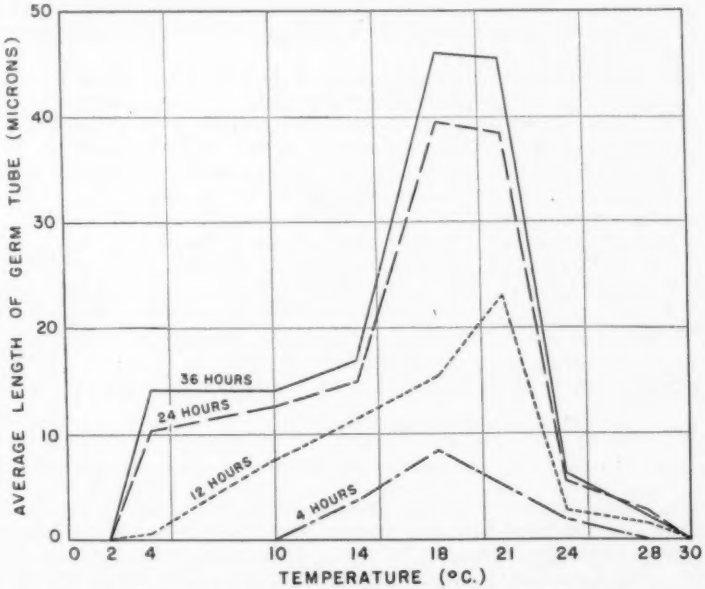

FIGURE 4.—Relation of temperature to conidial germination and germ-tube elongation.

When conidia in water are subjected to temperatures of 30° C. and above, the contents usually become vacuolate and one or both cells rupture, extruding their protoplasm into the surrounding liquid. Some of the spores remain intact at 30° but at higher temperatures (32° and 35°) practically all of them rupture. As stated above, conidia in hanging drops were held at the several temperatures for 48 hours. The conidia failing to germinate at 2°, 30°, 32°, and 35° were then placed in a 20° chamber. The spores formerly held at 2° now promptly germinated. A few of the conidia that had not ruptured at 30° also germinated. Those held at 32° and 35° were all dead. Those spores which germinated slowly at 4° were held at that temperature over a period of several days and were observed to continue to develop to a degree which would seem sufficient to

produce infection. This is of interest in view of the fact that the disease makes very rapid development on barley in the fall when temperatures are near and below freezing for periods of considerable duration.

Sporulation on the Host

The development of scald following artificial inoculation proceeds normally in the greenhouse during the winter under controlled temperatures ranging from 12° to 24° C. Leaf lesions typical of the disease are produced, but the fungus failed to produce conidia in appreciable numbers on all such lesions examined. It was found that the limiting factor in conidial production under greenhouse conditions was apparently the low humidity, for when plants bearing sterile lesions were placed in a glass-moist chamber of 95-percent humidity and controlled temperature the lesions became abundantly covered with conidia, while controls in the open house at the same temperature failed to fruit.

The production of conidia upon the host also seems to be affected by temperature. This relation was tested by placing diseased barley plants, found to be free of conidia, in a series of moist chambers (approximately 95-percent humidity) held at temperatures of 5°, 10°, 15°, 20°, and 30° C. After a period of 48 hours' exposure to these temperatures the lesions were examined for conidia. The results, although not quantitative, were striking. At 5° and 10° numerous conidia were produced, yet they were relatively few in contrast to the myriads to be obtained from plants held at 15° and 20°. At 30° no conidia could be found; however, at this temperature and high humidity the lesions were overrun by various saprophytes which may have influenced the scald organism. These temperature relations agree quite closely with those for germ-tube elongation, where the fungus is wholly inactive at 30° and, although somewhat retarded, effectively active at 5°.

Physiologic Specialization

Material and Methods

The inoculum (conidia and mycelial fragments) for most of the experiments reported here was secured from cultures of the organism on potato-dextrose agar slants. Except for one culture mentioned later, only monosporous cultures were tested. The conidia, which are formed in masses intermixed with mycelium, cannot readily be washed from the tubes. Therefore, the fungus mass was removed from the tubes, crushed to fine fragments with a spatula, then taken up with water and strained through cheesecloth to remove the larger fragments of mycelium. The inoculum was sprayed over the plants with an atomizer and allowed to dry. After drying of the inoculum, the plants tested in the greenhouse were reatomized with tap water and placed in a moist chamber held at 100-percent humidity and a temperature of about 20° C. The foliage was kept continuously wet for 48 hours, after which the plants were removed to the greenhouse bench. In some tests conidial inoculum was washed from diseased host plants. The sources of cultures used in these studies are given in table 1.

TABLE 1.—*Cultures of Rhynchosporium secalis and R. orthosporum tested in cross-inoculation studies, with host source and place of collection*

Species and culture no.	Host source	Place of collection	Date of collection	Collector
R. secalis:				
B11	Barley	Madison, Wis.	October 1926	Writer.
B21	do	do	October 1927	Do.
B31	do	do	do	Do.
B42	do	Corvallis, Oreg.	December 1928	H. P. Barss.
B51	do	Madison, Wis.	June 1929	Writer.
B62	do	do	November 1929	Do.
B71	do	Corvallis, Oreg.	March 1931	R. Sprague.
B82	do	Madison, Wis.	July 1932	Writer.
B10	do	Germany		H. Klebahn.
Hm11	*Hordeum murinum*	Corvallis, Oreg.	February 1934	R. Sprague.
Hj11	*H. jubatum*	Madison, Wis.	July 1935	Writer.
A13	*Agropyron repens*	do	October 1928	Do.
A2	do	do	June 1929	Do.
A41	do	Middleton, Wis.	July 1932	Do.
Br. 14	*Bromus inermis*	Madison, Wis.	October 1928	Do.
Br. 21	do	do	May 1929	Do.
Br. 51	do	do	June 1929	Do.
E. c. 13	*Elymus canadensis*	do	October 1928	Do.
E. c. 21	do	Fort Atkinson, Wis.	May 1929	Do.
E. c. 31	do	Madison, Wis.	June 1930	Do.
R. 11	Rye	do	October 1926	Do.
R. 21	do	do	October 1927	Do.
R. 31	do	do	May 1929	Do.
R. 41	do	do	May 1930	Do.
R. orthosporum:				
D11	*Dactylis glomerata*	do	May 1927	Do.
D21	do	Whitewater, Wis.	May 1929	Do.

The cross inoculations in the field were conducted similarly. After spraying the plants with inoculum from cultures they were covered for a 48-hour period with muslin tents, which were kept moist with a continuous fine spray of water, after which the tents were removed. Only seedling plants were tested in the field.

The host plants were inoculated in the greenhouse in various stages of maturity, ranging from seedling to flowering plants. The degree of maturity of the plants from the seedling to the flowering stage apparently has no effect on susceptibility of greenhouse or field-grown plants. No attempt was made to maintain a definite number of plants of a host species in the different trials. Generally from three to several plants, growing in one or more 4-inch pots, represented a host species in each inoculation series.

Symptoms on barley appear earlier than on the other hosts and are at maximum development 2 weeks after inoculation. On rye and on species of *Agropyron*, *Bromus*, *Elymus*, *Dactylis*, and *Hordeum* 3 weeks or longer may be required for full expression of the disease. Observations for infection were made at approximately weekly intervals, beginning 14 days after inoculation and continuing for 4 weeks.

The cross-inoculation studies have involved each of the host species from which cultures of the scald organism had been isolated by the writer as well as other species of the same genera and a number of species of other genera from which no cultures were available. The host species from which the cultures used in these studies were isolated serve to distinguish the physiologic races of the scald organism. Seed of the host species dealt with in table 2 were collected in the vicinity of Madison, Wis., or La Fayette, Ind.

TABLE 2.—*Greenhouse cross-inoculation studies with Rhynchosporium secalis and R. orthosporum* [1]

RHYNCHOSPORIUM SECALIS

Host[2] source of culture	Culture[3] designation	Date of inoculation	Results on differential hosts							
			Barley [4]	Rye [4]	*Agropyron repens*	*Bromus inermis*	*Dactylis glomerata*	*Elymus canadensis*	*Hordeum jubatum*	*Hordeum murinum*
Barley	B11	Jan. 15, 1927	+	−	------	------	------	------	------	------
	B31	Feb. 23, 1929	+	−	−	−	−	−	−	------
	B31	Apr. 6, 1934	+	−	−	−	−	−	−	−
	B31 [5]	May 14, 1934	+	−	−	−	−	−	−	−
	B42	Feb. 14, 1929	+	−	------	−	−	------	------	------
	B62	Mar. 15, 1930	+	−	------	−	−	−	−	------
	B71	Apr. 1, 1931	+	−	−	−	−	−	−	------
	B71	Apr. 10, 1934	+	−	−	−	−	−	−	−
	B82	Mar. 11, 1933	+	−	−	−	−	−	−	−
	B10	Apr. 11, 1934	+	−	−	−	−	−	−	−
	B10	May 18, 1934	+	−	−	−	−	−	−	−
Hordeum murinum	H.m. 11	Apr. 9, 1934	+	−	−	−	−	−	−	−
	H. m. 11	Apr. 29, 1934	+	−	−	−	−	−	−	+
	H. m. 11	Apr. 17, 1935	+	−	−	−	−	−	−	+
	H. m. 11	Feb. 15, 1936	+	−	−	−	−	−	−	−
Hordeum jubatum	H. j. 11	May 6, 1931	−	−	−	−	−	−	+	------
	H. j. 11	Feb. 27, 1933	−	−	−	−	−	−	+	−
	H. j. 11	May 10, 1934	−	−	−	−	−	−	+	−
	H. j. 11 [6]	May 12, 1934	−	−	−	−	−	−	+	−
Agropyron repens	A 13	Feb. 25, 1929	−	−	+	−	−	−	−	------
	A 13	June 26, 1934	−	−	+	−	−	−	−	−
	A 2	Mar. 12, 1930	−	−	+	−	−	−	−	------
	A 2	May 2, 1931	−	−	+	−	−	−	−	−
	A 41	Jan. 12, 1933	−	−	+	−	−	−	−	------
	A 41	Apr. 21, 1934	−	−	+	−	−	−	−	−
	A 41	May 19, 1934	−	−	+	−	−	−	−	−
Bromus inermis	Br. 14	Mar. 7, 1929	−	−	−	+	−	−	−	------
	Br. 21	Mar. 10, 1930	−	−	−	+	−	−	−	------
	Br. 51	Feb. 18, 1932	−	−	−	+	−	−	−	−
Elymus canadensis	E. c. 13	Mar. 19, 1929	−	−	−	−	−	+	−	------
	E. c. 21	Feb. 14, 1930	−	−	−	−	−	+	−	−
	E. c. 31	Feb. 24, 1932	−	−	−	−	−	+	−	−
	E. c. 31	Feb. 21, 1933	−	−	−	−	−	+	−	−
Rye	R 11	1929	−	+	−	−	−	−	−	------
	R 21	Mar. 7, 1920	−	+	−	−	−	−	−	------
	R 41	Feb. 28, 1931	−	+	−	−	−	−	−	------

RHYNCHOSPORIUM ORTHOSPORUM

Dactylis glomerata	D 11	Mar. 17, 1929	−	−	−	−	+	−	−	------
	D 11	Apr. 16, 1934	−	−	−	−	+	−	−	−
	D 21	Mar. 17, 1930	−	−	−	−	+	−	−	------
	D 21	Apr. 4, 1934	−	−	−	−	+	−	−	−

[1] Infection is indicated by a plus (+) sign; failure to infect by a minus (−) sign; no test made is indicated by leaders.
[2] All inoculum was produced in potato-dextrose agar culture except as stated in footnotes.
[3] All cultures except A 2 were derived from isolated single conidia.
[4] Oderbrucker barley (Wisconsin Pedigree 6) and Schlanstedt rye were used in tests made during the period 1927–30 and Oderbrucker (C. I. 182) and Rosen rye during the period 1931–35.
[5] Inoculum washed from leaves of infected barley.
[6] Inoculum washed from leaves of infected *Hordeum jubatum*.

RESULTS OF CROSS INOCULATION TRIALS

From tables 2 and 3 it is apparent that the cultures of *Rhynchosporium secalis* tested in this study represent six highly specialized physiologic races which can be distinguished by their ability to attack the six hosts rye, barley, *Agropyron repens*, *Bromus inermis*, *Elymus canadensis*, and *Hordeum jubatum*.

The race of *Rhynchosporium secalis* attacking cultivated barley (*Hordeum vulgare*) is represented here by a total of eight cultures from the States of Wisconsin and Oregon and one from Germany. In

these tests this race has been unable to attack any of the species inoculated except barley. No variation in host specialization occurred among the several cultures of this race. Two of them, however, cultures B71 from Wisconsin and B10 from Germany, produced symptoms more slowly than the others and fruited sparingly, while the others fruited abundantly when exposed to high humidities for 24 hours. The culture from *H. murinum* is apparently the same or a closely related form, appearing identical in its effect on barley and in addition attacking *H. murinum* in two of the four tests conducted. It is likewise similar to the barley race in culture. Neither the cultures from barley nor those from *H. murinum* were able to attack *H. nodosum* or *H. pusillum*. The field inoculation tests with the barley race are in agreement with the greenhouse tests. The barley varieties Oderbrucker and Wisconsin Pedigree 39 were susceptible to two cultures of the barley race, while two varieties each of rye, oats, and wheat were immune.

TABLE 3.—*Field cross-inoculation studies with Rhynchosporium secalis*

Grain and variety inoculated	Results with cultures from—							
	Barley				Rye			
	B21		B51		R21		R31	
	Leaves inoculated	Leaves infected	Leaves inoculated	Leaves infected	Leaves inoculated	Leaves infected	Leaves inoculated	Leaves infected
	Number	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
Barley:								
Oderbrucker	168	63	315	173	159	0	279	0
Wisconsin Pedigree 39	183	31	198	110	159	0	219	0
Rye:								
Schlanstedt	297	0	396	0	210	25	418	42
Rosen	288	0	330	0	189	38	366	39
Oats:								
Kherson	198	0	258	0	192	0	197	0
Swedish Select	183	0	174	0	171	0	240	0
Wheat:								
Marquis	192	0	278	0	231	0	276	0
Turkey	237	0	357	0	135	0	246	0

An experiment on overwintering of the scald organism reported below (table 4) provided another test of specialization of the barley race. In April and May 1927, barley and rye were exposed in a moist chamber to dead scald-infected leaves of barley that had lain in the open during the winter. This exposure resulted in a heavy infection of the barley and no infection of the rye.

A specific race of *Rhynchosporium secalis*, as represented by one culture from Madison, Wis., occurs on *Hordeum jubatum*. This race is distinct from that on cultivated barley and *H. murinum*. It attacked neither of these hosts nor any of the other hosts, here considered as differential species. It is, however, very aggressive in its attack of *H. jubatum*. It also attacks *H. nodosum* and *H. pusillum*.

A distinct race of *Rhynchosporium secalis* attacking rye is represented in these studies by three cultures, all collected near Madison. This race is able to attack only rye among the differential hosts. No other host species has been found to be susceptible. The field inoculations

with two cultures of this race showed Schlanstedt and Rosen rye to be susceptible, while two varieties each of barley, oats, and wheat were immune.

Agropyron repens is likewise attacked by a distinct specialized race of the scald fungus. Three cultures, two of which came from the vicinity of Madison and one from Middletown, Wis., represent the race. This race also attacks *A. tenerum* but none of the other differential species.

Three cultures from *Elymus canadensis* represent a distinct race of *Rhynchosporium secalis* attacking *E. canadensis* but none of the other differential species. *E. virginicus*, *E. striatus*, and *Agropyron tenerum* were also infected. This race is the only one studied which was found to be capable of attacking a host species of a genus other than that from which it was isolated.

TABLE 4.—*Scald infection resulting from contact of seedling barley and rye with dead overwintered, scald-infected barley plants*

Host plants exposed	Leaves exposed	Leaves infected	
	Number	*Number*	*Percent*
Oderbrucker barley	221	165	74.7
Schlanstedt rye	177	0	0.0

A separate race of *Rhynchosporium secalis* is specialized on *Bromus inermis* and other species of *Bromus*. Three cultures from the vicinity of Madison represent this race. While failing to attack any of the differential species other than *B. inermis*, this race has produced infection on *B. arenarius*, *B. lanuginosus*, *B. madritensis*, and *B. villosus*.

Two cultures of *Rhynchosporium orthosporum*, isolated from *Dactylis glomerata* collected at Madison and Whitewater, Wis., have been tested for pathogenicity on the differential hosts of the six races of *R. secalis* (table 2). Like the races of *R. secalis*, it shows a high degree of host specificity, being unable to attack any variety inoculated other than *D. glomerata*.

A number of additional species reported to be susceptible in Germany by Bartels (*1*), but from which no cultures were available, have been included in these inoculation studies with negative results. This group includes the species *Cynosurus cristatus*, *Holcus lanatus*, *Lolium italicum*, *L. perenne*, *Phleum pratense*, and *Poa pratensis*. These species proved to be immune to one or more cultures of each of the races of *Rhynchosporium secalis* included in this study with the exception of *C. cristatus*, which was not tested to the *Bromus* race. Bartels (*1*) also found *Agrostis stolonifera* to be susceptible, while the closely related or synonymous species, *A. alba*, was immune from all of the races tested in the present work.

CULTURAL CHARACTERS OF PHYSIOLOGIC RACES

One representative culture of each of five physiologic races of *Rhynchosporium secalis* and one of *R. orthosporum* have been compared in Petri dish cultures. Cultures of the race on *Hordeum jubatmu*

were not available when this comparison was made. The media used were potato-dextrose and malt agar containing 1.5 percent of Bacto agar and 2 percent of dextrose and malt extract, respectively. Each plate contained 40 cc of the medium. The plates were inoculated in the centers with approximately equal masses of mycelium from monosporous cultures of the several races growing on malt agar.

The type of growth upon the two media was similar for any one race, although all races grew more rapidly on the potato-dextrose agar. Two general types of growth were to be distinguished among the six cultures (pl. 4). *Rhynchosporium orthosporum* and races of *R. secalis* from rye, *Bromus inermis*, and *Elymus canadensis* grew out from the inoculum center in a uniform radial manner, while races from barley and *Agropyron repens* heaped up to form irregular masses of mycelium and conidia. Differences in pigmentation were marked between the several races. The colonies of the barley race soon darkened and within 2 weeks were almost black. The race from *A. repens* was quite similar to that from barley but retained a light-pink cast. Colonies of the races from *E. canadensis* and rye remained light in color, while the colony from *B. inermis* became brown and produced a brown pigment which stained the medium about the colony. *R. orthosporum* soon developed a very dark pigment. These characters are relatively constant for each race as described and appeared in all isolations obtained.

Differences in abundance of fructification are marked and constant between certain races, but this character may vary in different cultures of other races. In the variable races a culture may change from fruitfulness to near sterility or the reverse. The barley race is uniformly highly conidial and has never deviated from this character. Cultures of the *Agropyron* race were similar in this respect although somewhat less fruitful. The race from rye is distinguished by the production of very few conidia in all cultures obtained. The races from *Elymus canadensis* and *Bromus inermis* are notable for their variability, some cultures producing abundant conidia and others none. Furthermore, a fruitful culture of these races may change to almost complete sterility. Attempts to influence fruitfulness in cultures by variations in nutrients and pH of media, temperature, and light have been unsuccessful.

Morphology of Conidia of Physiologic Races

A comparative study has been made of the shape and size of the conidia of six physiologic races of *Rhynchosporium secalis* and of *R. orthosporum* as produced upon the host in nature and in culture. Fifty conidia of each race from the host, and the same number from 7- to 10-day-old, simultaneously grown, corn meal agar cultures, were measured and morphologically compared. Only mature conidia were considered, clearly evident septation being the criterion of maturity.

The conidia of the several races from the hosts proved to have no distinguishing features either in shape or size (table 5 and fig. 1). Thus *Rhynchosporium secalis* is a relatively homogeneous species as far as conidia from the hosts are concerned.

TABLE 5.—*Measurements of conidia from host plants and cultures of races of Rhynchosporium secalis and of R. orthosporum*"[1]

Species of fungus and hosts from which conidia and cultures were obtained	Length						Diameter					
	Maximum		Minimum		Mean±S.E.		Maximum		Minimum		Mean±S.E.	
	Host	Culture	Host	Culture	Host	Culture	Host	Culture	Host	Culture	Host	Culture
	μ	μ	μ	μ	μ	μ	μ	μ	μ	μ	μ	μ
R. secalis:												
Agropyron repens	18.9	16.2	11.7	9.7	15.0±0.28	13.2±0.28	3.6	4.7	2.2	2.5	2.7±0.07	3.8±0.10
Bromus inermis	18.4	21.6	13.0	16.7	16.9± .24	18.3± .17	4.7	4.9	2.9	2.7	4.0± .07	3.5± .06
Elymus canadensis	18.0	18.0	12.1	12.6	15.1± .32	14.2± .24	5.4	3.8	2.7	1.4	3.9± .02	3.1± .15
Hordeum jubatum	19.8	.....	12.6	.....	16.3± .04	.....	3.6	.....	2.7	.....	2.9± .08	.....
Barley	21.6	21.6	12.6	13.5	15.8± .21	17.1± .28	3.8	4.9	2.7	2.5	3.3± .05	3.2± .08
Rye	19.8	17.3	10.8	9.0	16.4± .27	12.7± .05	3.6	5.4	2.3	3.1	2.8± .11	4.1± .15
R. orthosporum:												
Dactylis glomerata	19.4	19.8	14.4	11.7	16.9± .18	16.0— .28	4.7	4.3	2.3	2.5	3.0± .03	3.1± .16

[1] Measurements were of 50 spore samples of conidia from both host and cultures. Conidia were produced in corn meal-agar cultures 6 to 10 days old.

This was not true, however, of conidia from culture among which marked and consistent differences between some races were evident. Thus the mean lengths of conidia of the barley and *Bromus inermis* races were 17.1μ and 18.3μ, respectively, while those of the *Agropyron repens* and rye races were 13.2μ and 12.7μ, respectively. The situation is reversed relative to diameter, those of the rye and *A. repens* races exceeding those of the barley and *B. inermis* races.

Discussion of Physiologic Specialization

Two workers in Germany have published the results of cross-inoculation studies with *Rhynchosporium secalis*, indicating that collections of this organism from several host species in Germany display no differences in host specialization. Heinsen (*12*) sprayed barley, rye, wheat, and oats with a conidial suspension of *R. secalis* both in the field and greenhouse and obtained heavy infection of barley and rye, light infection of wheat, and no infection of oats. The source of his conidia was not given. Therefore one cannot be certain that he was not dealing with a mixture of races. He reports, however, one apparent case of spread of scald from rye to barley in field plots. Bartels (*1*) conducted cross inoculations involving conidial inoculum taken directly from barley, rye, *Hordeum murinum*, and *Lolium perenne*, with which he inoculated the cereal hosts barley, rye, wheat, and oats, and grass hosts of the genera *Agropyron*, *Agrostis*, *Bromus*, *Cynosurus*, *Hordeum*, *Lolium*, *Holcus*, and *Phleum*. In addition, conidial inoculum from an agar culture, isolated from *Holcus lanatus*, was tested. He reported successful transmission of the disease from each of these conidial sources to each of the hosts tested, from which he concluded, therefore, that there were no specialized races of *R. secalis*. Brooks (*2*), in England, has stated that *R. secalis* on "wild grasses" "undoubtedly may be a source of infection to crop plants." A suggestion of nonspecialization in Oregon has been given by Barss [11] in a report that scald was more severe on rye following barley in the rotation than when following other crops.

[11] See footnote 5.

The writer's observations of scald in the field lead to the conclusion that very restricted host specialization exists in the species *Rhynchosporium secalis*. The following field records provide evidence.

June 6, 1928, Madison, *Agropyron repens* in a field of severely infected rye was uninfected; *Bromus inermis* in a patch of severely infected *A. repens* was uninfected, while at a distance of about a mile *B. inermis* was severely infected; *Hordeum jubatum* was uninfected although growing intermixed with infected *B. inermis*.

June 21, 1928, Madison, wheat plots adjacent to severely infected barley plots were uninfected. (Wheat has been reported to be susceptible once in Germany and once in Washington.)

July 7, 1930, Madison, abundant *Agropyron repens* and timothy growing in a severely scald-infected barley plot were uninfected. (Timothy has been reported to be susceptible in Germany.)

There appears to be no explanation of the extreme diversity between the results of Bartels (*1*) and Heinsen (*12*) in Germany and those of the writer. Only one culture of the scald fungus from Germany has been studied by the writer. This was secured from the Central-Bureau Voor Schimmelcultures with the statement by Prof. Joha. Westerdijk that it is "one of the strains with which Bartels worked." In the writer's test this strain, designated B10, appeared to be specialized, producing infection only on cultivated barley (table 2). It differs in pathogenicity from most of the American cultures of the barley race only in producing symptoms on the host more slowly and sporulating less abundantly. However, one American culture, B71, behaved similarly. In culture the Bartels strain failed to produce the characteristic black pigment in old cultures as do those from North America.

The only apparent difference in the technique used in the cross-inoculation tests of Bartels and those of the writer is that the former worked mainly with host-borne conidia while the latter mainly used conidia from culture. However, in one case, Bartels reported working with inoculum from a culture isolated from *Holcus lanatus*, and finding the plurivorous relation as with host conidia from other species. On the other hand, the writer, in one inoculation trial each with the *Hordeum jubatum* and barley races, used host-borne conidia and found the same specialized condition as determined with inoculum from culture. Likewise inoculum from overwintered, naturally infected barley failed to attack rye, although it heavily infected barley. Thus the source of inoculum, i. e., from culture or host plant, did not affect the results of either Bartels or of the writer and will not serve as an explanation of their diverse results. Only the further exchange of cultures can clear up the apparently anomalous situation of extreme host specialization of a species in North America and the absence of specialization in Europe.

LIFE HISTORY

Seasonal Cycle of Occurrence

Scald becomes evident in early spring on cereals and grasses in the North Central States as soon as the first green foliage appears. With favorable conditions for development, the disease becomes progressively more prevalent on barley and rye until ripening of the crop. In the fall, volunteer barley plants may be heavily infected. The same general cycle occurs on the grasses, the disease developing abundantly in spring and fall and but little during the high temperatures of July and August.

Overwintering

The means of overwintering of *Rhynchosporium secalis* in the Northern States has not been known. It has been stated (*1*) that the organism passes the winter in an active state upon winter grains, which might account for the overwintering of the rye race and races on perennial grasses but not that of the barley race in the spring barley region. Heinsen (*12*) reported the scald fungus to be capable of saprophytic development in the soil in the greenhouse wherein its viability was maintained for a 15-month period, after which seedlings grown in the infested soil developed the disease. Bartels (*1*) also found the organism to grow in soil and persist there for a period of 6 months. The writer has been unable to detect growth of the organism on greenhouse compost soil when inoculated with a suspension of conidia and mycelium of the barley race or to secure infection of barley grown in such soil.

The possibility of overwintering and spread of scald in or on the seed was investigated in 1931 by an extensive sowing of barley seed from a severely infected field, upon soil where no scald was known to have occurred. The seed was of Wisconsin Pedigree 6 barley, produced at Madison in 1930 on severely scald-infected plants. The planting was made at La Fayette, Ind., in April 1931. No scald appeared in this planting.

Definite evidence of overwintering of *Rhynchosporium secalis* upon dead volunteer barley plants in the field has been secured by the writer at Madison. During the winters of 1926–27 and 1927–28, examination of dead infected leaves at regular intervals failed to demonstrate the survival of conidia until spring. During April and May 1927, however, the exposure of young barley seedlings as they emerged from the soil to such infected barley plant refuse resulted in heavy infection (table 4). The seedlings were kept in a high-humidity chamber and frequently sprayed with water during this exposure to the plant refuse. Thus, abundant viable inoculum was present on the overwintered plant refuse even though no conidia could be found previous to the inoculation trial.

In April 1929, dead, scald-infected barley plants that had been kept in the open field during the winter were found to bear abundant conidia after being exposed to room temperature and high atmospheric humidity for a few days. It appears probable that overwintering is accomplished by the fertile stroma of the scald fungus which resumes the production of conidia when warm temperatures return in the spring.

The observations and culture studies of other workers and the writer have failed to demonstrate the existence of a perfect stage which might serve as a spring source of inoculum.

SUMMARY AND CONCLUSIONS

Scald caused by *Rhynchosporium* spp. attacks primarily the leaf blades and to a lesser extent the leaf sheaths of barley, rye, and a number of grasses in the United States. The symptoms of the disease are the appearance of darkened water-soaked leaf spots, usually of lenticular shape followed by a drying and bleaching of the lesions which develop typical dark-brown margins. The simultaneous occurrence of many water-soaked areas covered by a gray subcuticular mycelium produces the appearance of scalding.

Scald is widespread in Europe and North America and has been reported from Tunis, Argentina, Peru, and Australia. The disease is often of little economic importance but is severe in the Pacific Coast States where estimated losses have amounted to from 20 to 30 percent.

An emended description of the genus *Rhynchosporium* has been presented, based upon the distinctive fertile stroma and manner of sporulation of the type species, *R. secalis* (Oud.) Davis. The valid binomial of the scald fungus occurring on barley, rye, and a number of grasses is *R. secalis* (Oud.) Davis.

Scald of *Dactylis glomerata* L. is caused by a fungus species that is definitely a member of the genus *Rhynchosporium* but has cylindrical conidia, which differentiate it from *R. secalis*, which has apically beaked conidia. The new species on *D. glomerata* has been described here as *R. orthosporum* sp. nov.

At present *Rhynchosporium secalis* and *R. orthosporum* are the only legitimate species in the genus *Rhynchosporium* as here defined. *R. alismatis* (Oud.) Davis, occurring on *Sagittaria* and *Alisma*, is excluded from the genus *Rhynchosporium* since its conidia are borne on flask-shaped conidiophores and it lacks the characteristic fertile stroma of this genus.

A high degree of host specialization has been found within the species, *Rhynchosporium secalis*. Six specialized races were found which can be distinguished by their capacity or incapacity to parasitize the host plants, namely, *Secale cereale* (rye), *Hordeum vulgare* (barley), *Agropyron repens*, *Bromus inermis*, *Elymus canadensis*, and *H. jubatum* in greenhouse and field inoculations. The existence of specialized races also is evidenced in the natural occurrence of this fungus in the field. Each race has displayed some constant and distinctive characters in artificial culture.

The conidia of the different races of *Rhynchosporium secalis* produced upon the hosts showed no important morphologic differences, while in culture distinct and constant differences between certain races were evident both in form of conidia and cultural characters.

Conidial germination proceeds readily in distilled water, occurring within the temperature range 4° to 28° C. The optimum temperature for germ-tube elongation lies between 18° and 21°. In distilled water, at and above a temperature of 30°, the conidia rupture and extrude the cytoplasm into the surrounding medium.

Fructification of the fungus is inhibited at the low relative humidities afforded by the greenhouse in winter, but occurs abundantly at high humidities.

Parasitism of barley by *Rhynchosporium secalis* is initiated by direct penetration of the leaf cuticle from appressoria, the mycelium establishing itself and making its initial development in the subcuticular position.

The enlargement of the infected area is accomplished by spread of the subcuticular mycelium. The epidermal cells collapse under the subcuticular mycelium being the first tissue to show the effects of the disease. Following epidermal collapse, the mycelium repeatedly penetrates from the subcuticular position into an intercellular position within the mesophyll, causing almost immediate collapse of that tissue. Relatively sparse development of mycelium occurs in the mesophyll tissue.

The subcuticular mycelium proliferates and enlarges, pushing the cuticle away from the epidermal wall, to form a fertile stroma, from

one to several cells in thickness, on the lesion surface. Fructification follows on the fertile stroma, covering the collapsed area of the lesion. Conidia are borne directly on the sides of the cells of fertile stroma on the surface of the lesion.

The barley race has been shown to overwinter in Wisconsin on dead tissues of plants infected during the previous season.

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THE BIOLOGY OF PLATYGASTER HERRICKII, A PARASITE OF THE HESSIAN FLY [1]

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INTRODUCTION

Platygaster herrickii Packard [3] is an important parasite of the hessian fly, *Phytophaga destructor* (Say), in certain sections of the United States. Little has been published on it except from the taxonomic point of view. In 1933 Gahan (*1*) [4] gave a history of the literature together with a full redescription of the adult. Valuable unpublished observations on its behavior and development were made as early as 1916, by the late W. R. McConnell, and descriptions of egg, first-instar larva, and methods of oviposition were deposited by him in official files of that year. The senior author began observations of its morphology and activity in the eastern coastal States in 1920, and since then has accumulated information as he has had the opportunity. More recently the junior author began work on the occurrence and habits of this parasite in the West Central States.

DISTRIBUTION AND ECONOMIC IMPORTANCE

Platygaster herrickii has been collected from most of the winter-wheat-growing sections of the United States (fig. 1). It is an important parasite of the first spring brood of the hessian fly in the southeastern portion of the wheat-growing sections and west of the Mississippi River in parts of Missouri, Iowa, Kansas, Nebraska, and Oregon. Parasitization by this species has been found to be as high as 25 percent of the host puparia in North Carolina, 20 percent in the extreme southern part of Virginia, and 3 percent in central Virginia. North of latitude 38° in the eastern coastal States little parasitization has been observed. Surveys made in 1931 and 1932 showed 36 percent parasitization by this species in southwestern Iowa, 14 percent in Missouri, 6 percent in Nebraska, and 1 percent in northeastern Oklahoma. In Oregon, Rockwood (*10*) has reported *P. herrickii* as parasitizing large numbers of hessian flies, but he says that it appears to be more susceptible to desiccation than either its host or the serphoid parasite *P. hiemalis* Forbes. Reeher found, in the vicinity of Forest Grove, Oreg., in 1930 an average of 14 percent parasitization by this species, with a maximum of 33 percent in one field, and in 1931 an average of more than 16 percent.

In the regions of its greatest abundance *Platygaster herrickii* usually occupies more species of hosts than do any of the other hessian

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[3] Order Hymenoptera, superfamily Serphoidea.
[4] Reference is made by number (italic) to Literature Cited, p. 213.

fly parasites except *Eupelmus allynii* (French), and, in terms defined by Smith (*12*), it is "extrinsically superior" to them. However, as it is practically defenseless against the typical chalcidoid parasites when competing with them in the same host, it may be considered as "intrinsically inferior" to all the principal chalcidoids.

As a supplementary parasite *Platygaster herrickii* is important largely for two reasons: (1) It works abundantly in those sections of the South and West where another important serphoid parasite of the hessian fly, *P. zosine* Walker, fails to thrive, and thus helps to maintain a higher degree of parasitization than would otherwise be possible; and (2) by ovipositing in the egg instead of the later stages of the host, as do the chalcidoids, it is able to parasitize hosts that later in the season become inaccessible to chalcidoid attack.

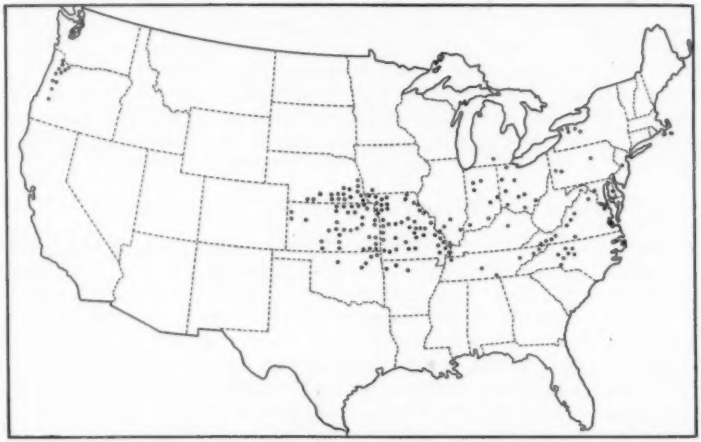

FIGURE 1.—Geographical distribution of *Platygaster herrickii*. Dots show localities where specimens have been collected.

TECHNIQUE

Specimens were studied in toto while alive in normal salt solution or Ringer's solution and also after having been killed and fixed in Bouin's fluid. Parasitized host larvae for sectioning were fixed in Bouin's fluid. Most of the parasitized host eggs, however, were fixed in Hermann's fluid or Flemming's solution, which stained them black and rendered them easier to handle in embedding and sectioning. Further to facilitate handling, several eggs at a time were tied up in tiny, fine muslin bags before being passed through the reagents prior to embedding. The paraffin method was used with a Minot rotary microtome. Iron haematoxylin was used for staining the microtomic sections illustrated in figure 5, *B* to *H*, and chloral haematoxylin counterstained with orange G for those illustrated in figure 6, *A* to *H*.

THE ADULT [5]

GENERAL APPEARANCE AND SEX DIFFERENCES

The adult (fig. 2, *A*) is approximately 1.5 to 2.2 mm long, and shiny black with grayish pubescence. The ovipositor is curved, slender, slightly attenuated, and each sheath valve (third valvula) (fig. 5, *K*) bears seven setae near its extremity and three hyaline tubercles distributed along its distal half. The dark sclerotic portion of the sheath ranges in length from 0.33 to 0.44 mm.

The sexes may be differentiated by the antennae (fig. 2, *B*), the second joint of the flagellum being broader in the male than in the

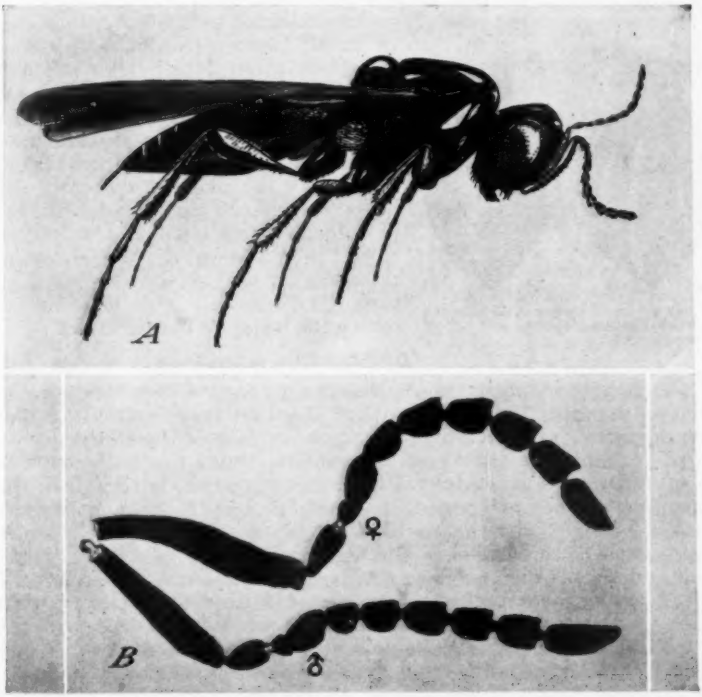

FIGURE 2.—*Platygaster herrickii: A,* Adult female, ×32; *B,* male (♂) and female (♀) antennae, ×85.

female, and by the shape of the abdomen, which is distinctly pointed in the female, whereas in the male it is more spatulate and the tip curves more definitely downward. The wings protrude farther beyond the tip of the abdomen in the male than in the female.

COMPARISON WITH OTHER SERPHOID PARASITES OF THE HESSIAN FLY

Platygaster herrickii can be distinguished from the other serphoid parasites of the hessian fly, *P. zosine* and *P. hiemalis*, by its distinctly larger size and the presence of conspicuous parapsidal grooves. It is

[5] For a technical description of the adult refer to Gahan's (*1*) redescription published in 1933.

about the same size as and in many respects resembles both *Trichacis remulus* (Walker) and *Platygaster pleuron* (Walker). It may readily be distinguished from *T. remulus* by the absence of the tuft of short gray hairs near the apex of the scutellum which characterizes the latter parasite, and it differs distinctly from *P. pleuron* by the absence of the many longitudinal striations along the basal half of the dorsal and ventral surfaces of the abdomen (fig. 3). The face of *P. herrickii* is so faintly punctate as to appear smooth and shiny except for coarse rugulations near the base of the antennae, while the face of *P. pleuron* is closely and distinctly punctate and has no conspicuous rugulations.

The ovipositor also distinguishes *Platygaster herrickii* from these other serphoids, although there is a marked resemblance in all except *P. zosine*. As in the case of *P. herrickii*, each ovipositor sheath valve of both *P. hiemalis* and *Trichacis remulus* bears only three of the hyaline tubercles, but the entire ovipositor of *P. hiemalis* is only about one-third as large as that of *P. herrickii*, and in *T. remulus* the tubercles are placed much closer together. In *P. pleuron* the ovipositor sheath valve bears five or six hyaline tubercles instead of three, a distinct point of differentiation. In *P. zosine* the ovipositor is a third smaller, with sheath valves straight instead of curved, and blunt at the extremity instead of attenuated.

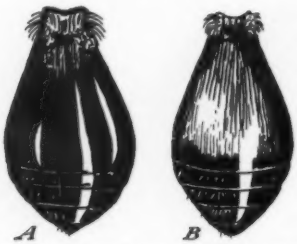

FIGURE 3.—Dorsal surface of the abdomen of (*A*) *Platygaster herrickii* and (*B*) *P. pleuron*. ×37.

OVIPOSITION

The female oviposits in the hessian fly egg. The host eggs are slender, reddish, rod-shaped, about 0.4 mm long, and are usually found sparsely scattered over the upper surface of the wheat leaves.

In searching for the eggs, the parasite walks hurriedly over the wheat leaves and constantly vibrates her antennae, letting their tips brush the surface of the leaf. Upon striking a hessian fly egg she strokes it rapidly with the tips of both antennae for about half a second. Then, with body parallel to the length of the egg, she draws herself over and a short distance beyond it and feels about for it with the tip of her extended ovipositor. Sometimes she misses the egg entirely and walks away, but more often she finds it and inserts the ovipositor into its upper surface. While depositing an egg she stands with head and antennae down, wings folded over the back, and motionless except for a slight rhythmic movement of the abdomen. She appears to oviposit quite as readily when facing downward as when facing upward on the leaf.

Two females were timed for the number of seconds the ovipositor was held in a host egg. In 30 ovipositions the time was found to range from 5 to 20 seconds, with an average of 14.

Host eggs freshly oviposited into by *Platygaster herrickii* showed only a single egg per insertion, and observations made by the late W. R. McConnell agree with this.

HABITS AND OTHER CHARACTERISTICS

When emerging from the host, the parasite makes a circular or irregular hole from 0.5 to 0.7 mm in diameter near one end of the puparium (fig. 4).

An examination of 200 *Platygaster herrickii* adults, taken at random from eight localities in Missouri, three in Nebraska, and one in Kansas, showed 102 females and 98 males, which indicates the sex ratio to be nearly equal.

Platygaster herrickii is capable of parthenogenetic reproduction, and, as is well known, this results in male offspring only.

The adult *Platygaster herrickii*, when molested, appears to feign death, drawing its legs and antennae up close to the body, although in actual death the antennae and legs are stretched away from the body. If disturbed while crawling over the wheat leaves, it quickly drops to the ground. It is positively phototropic, as demonstrated by its behavior under the writers' observation for many years.

FIGURE 4.—Hessian fly puparium showing exit hole through which an adult *Platygaster herrickii* has escaped. × 22.

THE EGG AND EMBRYONIC DEVELOPMENT

DESCRIPTION OF EGG AT TIME OF OVIPOSITION

The egg (fig. 5, *A*) of *Platygaster herrickii* is hyaline, highly refractive, and immediately after oviposition is 0.06 mm long and 0.03 mm wide. It is subellipsoidal, with the caudal extremity slightly attenuated and usually turned a little to one side. The cephalic end is well rounded, with two or three short, flagellumlike, follicular adherencies.

EMBRYOLOGICAL DEVELOPMENT

The parasite egg develops simultaneously with that of its host. A sagittal section of a host egg with a freshly deposited parasite egg lying within it is shown in figure 6, *C*. Figure 5, *B*, depicts the same parasite egg greatly enlarged and shows the position of sperm and nucleus. An egg 3 hours old, showing the appearance at first maturation, is illustrated in figure 5, *C*, and eggs 3 days old, which have reached the four-cell cleavage stage, in figure 5, *D* and *E*. The development so far described is essentially like that of *Platygaster hiemalis* Forbes and *P. vernalis* (Myers) (=*P. zosine* Walker) as related by Leiby and Hill (*5*, *6*), except that at the time the embryonic nuclei (*em*) reach the four-cell cleavage stage the paranuclear mass (*pa*) within the trophamnion (*tro*) has not yet broken up into the several small distinct masses such as are usually found in *P. zosine*.

The embryo continues to develop in monembryonic manner, rather than by polyembryony as in the case of *Platygaster zosine* or by twinning as does *P. hiemalis*. Successive advancements of development in the morula and blastula forms are shown in figure 5, *F*, *G*, and *H*, and figure 6, *A*. These stages are similar to those shown by Silvestri (*11*) for *P. dryomyiae* Silv., and to those of the monembryonic forms of *P. hiemalis* as shown by Leiby and Hill (*5*). *P. herrickii*, however, does not accumulate about itself an adventitious cyst of host tissue as do these other species of *Platygaster*.

PSEUDOGERMS

Beginning with the blastula stage, an interesting demarcation of development takes place in the paranuclear body of the trophamnion. During the period of blastula formation this body becomes broken

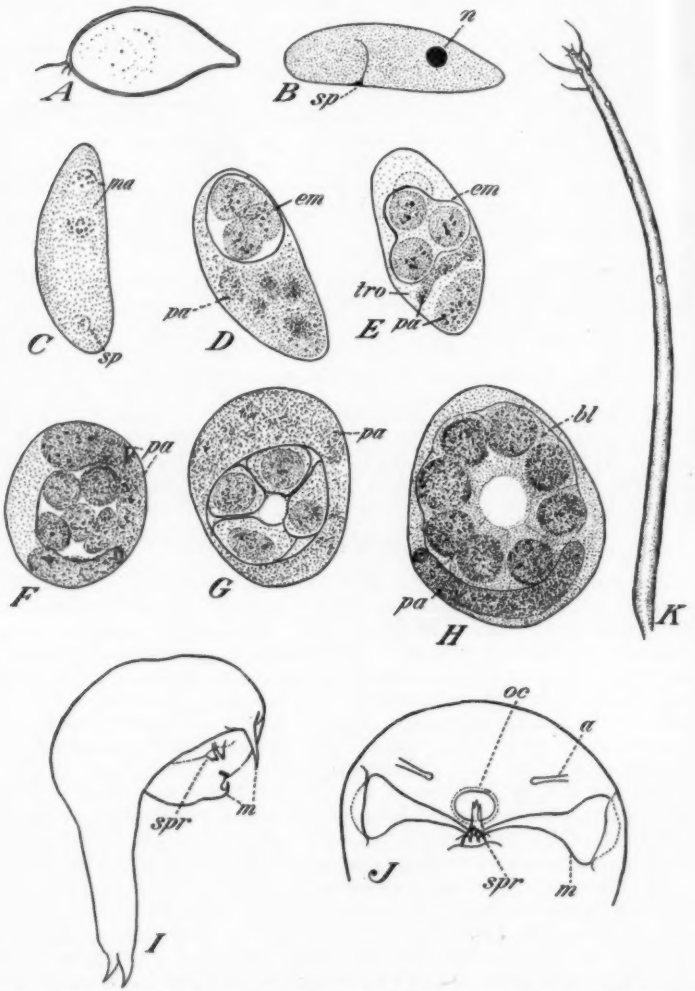

FIGURE 5.—*Platygaster herrickii: A*, Freshly deposited egg, × 433; *B*, sagittal section of freshly deposited egg with nucleus (*n*) and sperm (*sp*), × 1,306; *C*, egg 3 hours old showing sperm or male nucleus (*sp*) and first maturation stage (*ma*), × 1,050; *D* and *E*, eggs 3 days old showing embryo (*em*) at the four-cell stage of division, paranuclear mass (*pa*), and trophamnion (*tro*), × 970; *F*, section of egg 2 days old in morula stage, with paranuclear mass (*pa*) beginning to break up, × 1,087; *G*, section of egg 4 days old beginning to show blastula characteristics, × 1,000; *H*, section of another egg 4 days old showing distinct blastula formation (*bl*) and a well-defined paranuclear mass (*pa*), × 974; *I*, dorsal aspect of primary larva with head bent forward in normal position, showing mandibles (*m*) and sclerotic projection (*spr*) on inferior lip, × 273; *J*, ventral aspect of head, showing antennae (*a*), oral cavity (*oc*), mandibles (*m*), and sclerotic projection (*spr*) on inferior lip, × 314; *K*, sheath valve of ovipositor, × 270.

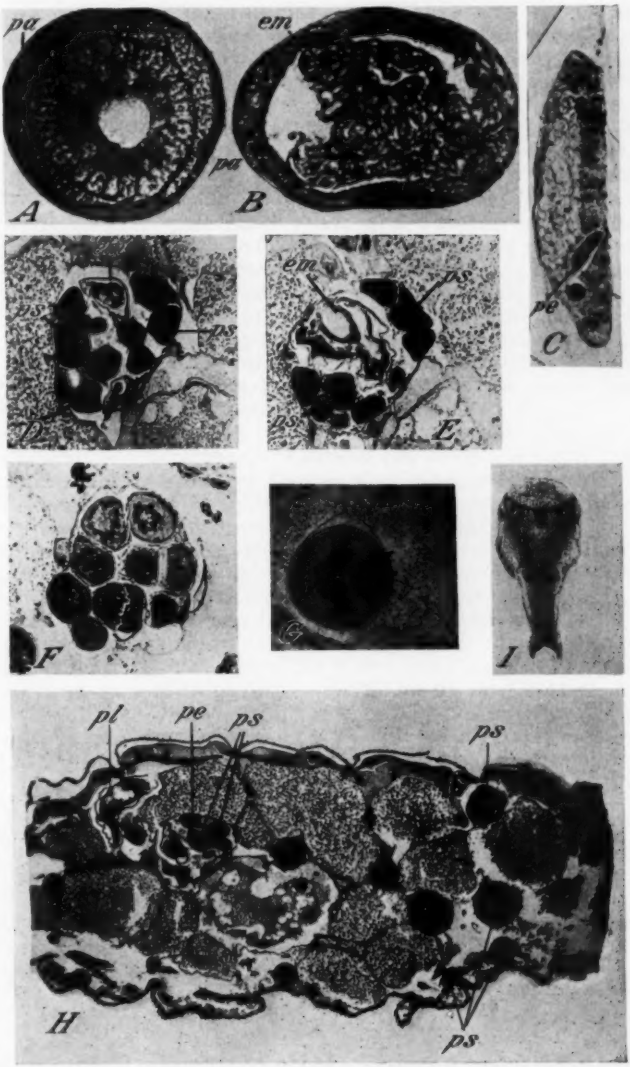

FIGURE 6.—Photographic studies [6] of *Platygaster herrickii*: *A*, Microtomic section of egg in advanced blastula stage, showing paranuclear mass (*pa*) breaking up into several bodies, × 425; *B*, section of egg showing embryo (*em*) in advanced stage of development and paranuclear mass (*pa*) divided into numerous small bodies, × 350; *C*, sagittal section of a host egg with a freshly deposited egg (*pe*) lodged within × 241; *D* and *E*, sections at different points through a parasitic body with embryo (*em*) about ready to hatch and pseudogerms (*ps*) which have commenced precocious development, × 116; *F*, section through a cluster of pseudogerms shortly after the larva has hatched, × 106; *G*, cross section through a single pseudogerm, × 131; *H*, sagittal section through a portion of a hessian fly larva showing parasite egg (*pe*) in an advanced stage of development with pseudogerms greatly enlarged, a primary larva (*pl*) that has recently hatched from another egg, and pseudogerms (*ps*) released from this egg and scattered about in the body cavity of the host, × 55; *I*, ventral aspect of entire primary larva. × 94.

[6] Photomicrographs made by E. J. Udine.

up (fig. 6, *A*), and as the embryonic development progresses many distinct bodies appear (fig. 6, *B*). In the individual illustrated (fig. 6, *B*) the embryonic membranes are forming and the paranuclear mass has already divided into many nuclei. Some of the best defined ones are oval and 0.016 mm long. At this stage the paranuclear bodies begin a precocious development, and since they superficially imitate the development of true germs the writers will call them "pseudogerms", as Marchal (*8, p. 600*) has called similar bodies in other species of *Platygaster*.

Two sections through a parasite larva fully formed and about ready to hatch are shown in figure 6, *D* and *E*. It may be observed that the paranuclear bodies have increased considerably in size. Measurements showed them to range from 0.03 to 0.06 mm in length. Moreover, nucleated masses of chromatin have become distinctly visible in each body. These bodies continue to grow after the egg has hatched, and the granules of chromatin become large and either grouped in the center of the body or arranged in blastulalike formation. Figure 6, *F*, shows a section through a group of pseudogerms that are still clinging together within a partly ruptured chorion through which the larva has broken in the process of hatching. The pseudogerms in this group were larger than those shown in the earlier embryonic development, measuring from 0.057 to 0.086 mm in diameter. In this case the newly hatched larva was lodged nearby in the body cavity of the host. The pseudogerms finally break loose entirely and become distributed throughout the body cavity, as shown in figure 6, *H*. At this stage they are spherical and protected by a chorionlike wall. They continue to increase in size while loose in the body cavity of the host. Measurements of 176 pseudogerms taken at random from numerous hosts under natural field conditions and examined in physiological media showed diameters ranging from 0.04 to 0.33 mm, with an average of 0.14 mm. Figure 6, *G*, is a section through the center of a typical pseudogerm that measured 0.13 mm in diameter after fixation. This section shows the disposition of chromatin particles and the chorionlike protecting wall.

No true embryonic development of a pseudogerm was ever observed, and examinations, later in the season, of parasitized hessian fly puparia from the field showed the pseudogerms in the process of disintegration, and eventually consumed by the parasite larva.

Out of eight flies parasitized in the field in which there was but one first-instar larva, the number of pseudogerms was found to range from 12 to 38, with an average of 25. In 54 cases in which more than one larva was found in a single host, the average was 22 pseudogerms per embryo. The maximum number found in any host was 145, and judging from the larvae present in this host, these were the product of six eggs.

Figure 6, *H*, shows a sagittal section of part of a hessian fly larva containing in its body cavity a parasite egg (*pe*) with the embryo about ready to hatch, and pseudogerms (*ps*) still retained within the body walls of the parasite. Nearby is a primary larva (*pl*) that has recently hatched and released a number of pseudogerms (*ps*) which have grown and become distributed throughout the body cavity.

The development of pseudogerms of this character was first discovered by Marchal (*8*), who found them occurring in *Platygaster lineatus* Kief., *P. marchali* Kief., and *Trichacis remulus*. In all these

species the pseudogerms, like those of *P. herrickii*, represent precociously developed paranuclear bodies of the trophamnion and are released into the body cavity of the host when the primary larva liberates itself from the embryonic mass. In these species they differ, however, from those of *P. herrickii* in that after liberation they not only grow but multiply.

The pseudogerms described by Parker (*9*) for the braconid parasite *Macrocentrus gifuensis* Ashmead differ somewhat from those found in conjunction with the species of *Platygaster*. With *M. gifuensis*, which is polyembryonic, the pseudogerms are released into the body cavity of the host during the development and dissociation of the morulae, instead of at the end of embryological development, and they are usually associated with parts of the trophamnion instead of being confined to the paranuclear masses.

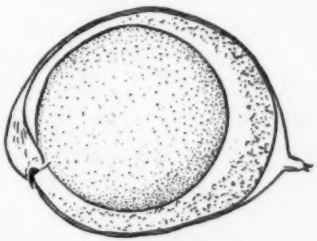

FIGURE 7.—Lateral aspect of primary larva of *Platygaster herrickii* in an advanced stage of growth. × 135.

The occurrence of these pseudogerms affords a valuable aid in identifying *P. herrickii* in its early stages, for, with the exception of *Trichacis remulus*,[7] this is the only hessian fly parasite in the United States known to produce such bodies. *T. remulus*, however, may be identified by the primary larvae, which offer marked distinguishing characteristics.

THE PRIMARY LARVA

The young larva (fig. 5, *I* and *J*, and fig. 6, *I*) is colorless and translucent. A typical specimen measured 0.288 mm in length when extended and 0.130 mm across its greatest width. It is cyclopean in form, with the cephalic region slightly longer and considerably wider than the caudal region. The caudal extremity is bifurcated with two pointed, backward-curving hooks. Two-thirds of the way forward on the abdomen there is a well-defined joint at which the caudal region may be bent forward under the head. The mandible is 0.036 mm long and curved near the extremity. The buccal opening is circular, and the inferior lip bears two small, closely packed groups of tiny sclerotic projections, one group at the edge of the buccal opening and the other on a short, elevated sclerotic ridge just caudad of the first group. These projections vary in number and size. In one specimen examined there were four such in the first group and nine in the second group; in another, three and seven, respectively. The extremities of the mandibles, when brought together, rest between the two groups. Two slender, slightly knobbed antennae, 0.013 mm long, are present a short distance in front of the mandibles.

In its advanced development (fig. 7) the primary larva is almost spherical and several times its original size. The caudal appendage becomes functionless and eventually collapses.

Frequently two or more first-instar larvae are found in a host, but only rarely does more than one reach maturity. In a few instances two adults have been reared from the same host and in one case four pupae were found in one host.

[7] *Trichacis remulus* was introduced into the United States from France in 1935.

The primary larva of *Platygaster herrickii* can readily be distinguished from those of *P. zosine* and *P. hiemalis* because neither of these species is cyclopean in form. *Trichacis remulus*, as described by Marchal (*7*, *8*), is conspicuously different from *P. herrickii* in having footlike processes at the base of the head, and in the shape of the antennae. The senior writer, however, noted a striking resemblance to *P. pleuron*, although there seemed to be a slightly different arrangement in the sclerotic projections on the inferior lip.

References to the larval form of *Platygaster herrickii* were made by Kulagin (*4*) in 1898 and by Hill (*3*) in 1926. Kulagin, however, was incorrectly identifying an entirely different species, as has been pointed out by both Marchal (*8*, *p. 490*) and Hill (*3*).

THE MATURE LARVA

The mature larva (fig. 8) is white, shining, and somewhat reniform. A typical specimen was 2.1 mm long and 0.9 mm wide. There are 11

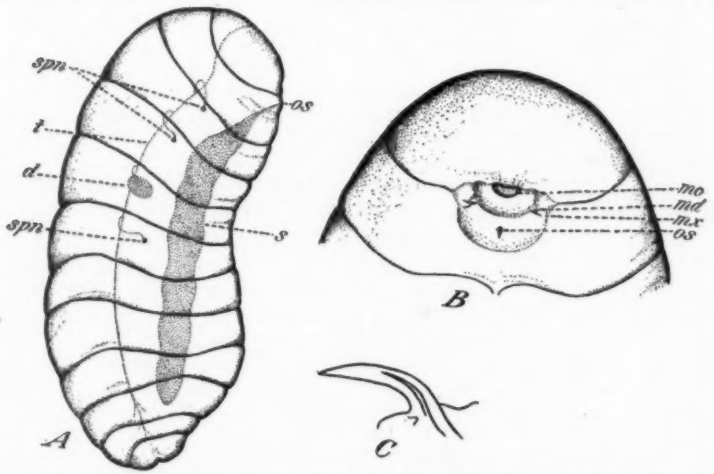

FIGURE 8.—Mature larva of *Platygaster herrickii*: *A*, Lateral aspect showing segmentation of body, spiracles (*spn*), lateral branch of tracheal system (*t*), discoidal body (*d*), lateral branch of silk gland (*s*), and silk-gland opening (*os*), × 33; *B*, head and part of thorax showing mouth (*mo*), mandibles (*md*), sclerotic ridge on maxillary area (*mx*), and silk-gland opening (*os*), × 77; *C*, mandible, × 450.

well-defined body segments, excluding the head. Spiracles are present on the second and third thoracic segments and the second abdominal segment. On each side of the first abdominal segment there is a large discoidal body[8] (fig. 8, *A*, *d*) under the cuticle at the terminus of the lateral tracheal branch. The buccal opening (fig. 8, *B*, *mo*) is a simple crescent-shaped orifice capable of being opened or closed by the soft superior lip controlled by radiating muscles. The mandibles (fig. 8, *B* and *C*) are 0.0466 mm long, slightly curved, and darkly sclerotic. They occur somewhat posterior to the mouth and are widely separated. In one specimen their bases were 0.2 mm apart. Each of the maxillary areas bears a sclerotic ridge (fig. 8, *B*, *mx*) immediately posterior to the mandibles. The silk-gland opening

[8] This body is characteristic of many species of *Platygaster* and has been described by Hill (*2*, *3*) as occurring in *P. zosine* (*P. vernalis*) and *P. hiemalis*, by Marchal (*8*) in *P. ornatus*, and by Silvestri (*11*) in *P. dryomyiae*. Its function is obscure, although Silvestri calls it a gland.

(fig. 8, *A* and *B*, *os*) lies on the median line posterior to the mandibles. The silk glands (fig. 8, *A*, *s*) are two single tubes, one extending along each side of the body as far as midway of the sixth abdominal segment.

During this stage most of the host contents are consumed, but not until the host has formed its dark puparium.

The mature larva resembles those of the other serphoid parasites of the hessian fly, although the mandible of a specimen of *Platygaster pleuron* was found to be slightly longer than that of *P. herrickii*. According to Marchal (*7*), the mandibles of *Trichacis remulus* are sharply curved and borne on two large tubercles, which is not the case in *P. herrickii*. The mature larva of *P. herrickii* is about twice as long as that of *P. zosine* and the mandibles are longer by 0.016 mm. This may seem a small difference, but in both species the dimensions of the mandibles have been found to be constant. The larval body of

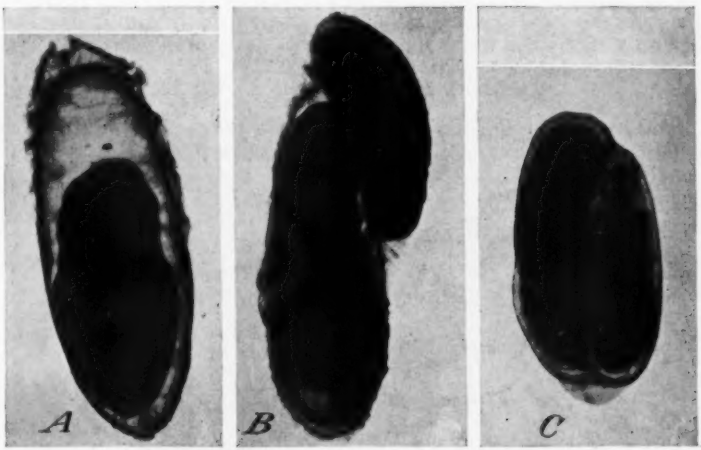

FIGURE 9.—Photomicrographs of *Platygaster herrickii*: *A*, Cocoon with larval skin of host adhering to the outside; *B* and *C*, examples of two cocoons found in a single host, greatly enlarged.

P. herrickii is also about twice as large as that of *P. hiemalis*, with mandibles slightly longer and distinctly more curved.

THE COCOON

The cocoon of *Platygaster herrickii* is made of straw-colored, thin, shiny, tough, elastic material. It is ovoid in shape and varies somewhat in size. Ten specimens ranged from 2.17 by 0.87 mm to 3.22 by 1.31 mm, with an average of 2.87 by 1.12 mm. The cocoon usually occurs singly within the host puparium, which it nearly fills, but two and even three cocoons have been found in one host. Figure 9 shows (*A*) a cocoon removed from the host puparium but still within the host skin and (*B* and *C*) two cocoons in one host.

THE PUPA

The pupa (fig. 10) is white when first formed, as in other Hymenoptera, but it soon darkens. Beginning with the compound eyes, the color spreads until finally the entire body, except the thin integument between the abdominal plates, becomes shiny black.

SUPERPARASITISM

Superparasitism appears to be common with this species. Females in the laboratory cages oviposited into eggs that had already been parasitized by other females. They also oviposited repeatedly into the same egg, three or four ovipositions being observed frequently. Out of 20 parasitized hessian flies taken from a field near Salisbury, N. C., 12 contained more than one larva per host, distributed as follows:

Larvae	*Occurrences*	*Larvae*	*Occurrences*
1	8	4	2
2	3	6	2
3	4	8	1

The occurrence of more than one larva per host apparently is not due to polyembryony, for no evidence of polyembryony was found in the embryological studies. Furthermore, in many hundreds of rearings only rarely did more than one adult develop in a host.

SEASONAL HISTORY AND MORTALITY

Platygaster herrickii has one generation a year. The adults emerge in the spring simultaneously with the hessian flies and oviposit into

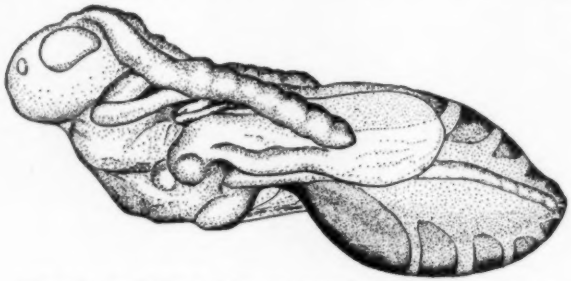

FIGURE 10.—Pupal stage of *Platygaster herrickii* before it has hardened. × 35

their eggs. The parasite eggs hatch and reach the primary larval stage in the course of a few weeks, and by the end of the summer the larvae are full grown. The cocoon is soon formed, pupation takes place, and the adult stage is attained before winter. The adults hibernate within the cocoons inside the host puparium until warm spring weather induces emergence.

Material from Abington, Va., examined on June 30 contained only embryos, but by July 12 primary larvae were found, and on July 15 one mature larva. Other material collected at the same locality on August 17 showed *Platygaster herrickii* predominant in the primary larval stage, although again one full-grown larva was discovered. By August 24 primary and mature larvae and white pupae were found, and by September 9 white pupae and one fully developed adult were present within their cocoons.

In the vicinity of Wichita, Kans., *Platygaster herrickii* was found ovipositing throughout most of April. Mature larvae appeared the latter part of July, and cocoons were formed in August. White pupae

were found by September 1, which became black by September 14 and transformed to unemerged adults by November 25. Dissections made the last of September showed parasites in all stages of development from embryos to black pupae.

Reeher says that in the vicinity of Forest Grove, Oreg., adults of this species begin to emerge, in normal years, about the middle of April, although an occasional individual may appear as early as March 26. They may be found in the fields for about a month, coincident with the normal spring emergence of the hessian fly. Examination of *P. herrickii* material taken from the fields near the

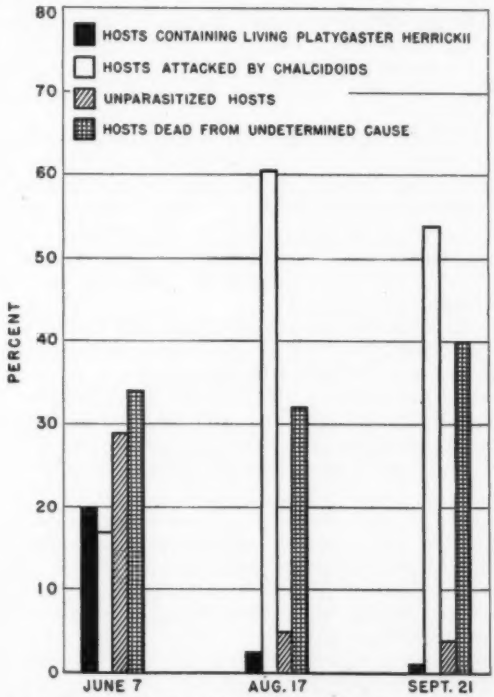

FIGURE 11.—Observations on parasitization of hessian fly puparia collected at Abingdon, Va., on three different dates in the summer of 1932, indicating mortality of *Platygaster herrickii*.

end of October showed cocoons to be already formed and usually the adult stage present within. As in the other parts of the country, hibernation normally takes place in the adult stage within the cocoon.

Platygaster herrickii parasitizes its host at the beginning of the season, before most of the other parasites have begun their work, and consequently comes into competition with all other species that attack the immature stages of the hessian fly. At a result of this multiple parasitism a high percentage of *P. herrickii* succumb during the season. This was shown by an examination of hessian fly puparia collected from a wheatfield near Abingdon, Va. Collections of 200 puparia were made on June 7, 220 on August 17, and 300 on September

21. These puparia were dissected and their contents observed. Figure 11 illustrates the increasing mortality of *P. herrickii* during the season. It will be observed that this was due chiefly to the inroads of chalcidoids and to some extent to undetermined factors. Hosts attacked by chalcidoids increased from 17 percent on June 7 to 60.5 percent on August 17. By September 21 other conditions interfered sufficiently to leave only 54 percent recognizable as attacked by chalcidoids. Those dead from undetermined causes increased from 34 percent in June to 40 percent in September. The decrease of 2 percent in August can be ignored as due to unavoidable deviations between samples. Consequently, not only were unparasitized hosts reduced from 29 percent in June to 4 percent in September, but those containing living *P. herrickii* were likewise reduced from 20 percent in June to 2.5 percent in August and to 1 percent in September, showing a total mortality of 95 percent of *P. herrickii* during the season.

The species of Chalcidoidea involved were *Eupelmus allynii*, *Merisus destructor* (Say), *Tetrastichus carinatus* Forbes, and *Merisus febriculosus* Girault. The number of the last two was insignificant, but *E. allynii* formed 10 percent of the total on June 7 and 39 percent on August 17. The proportion of *M. destructor*, which was 6 percent on the first dissection, had increased to 10 percent by August 17. Much of the mortality of *P. herrickii* in the vicinity of Abingdon may therefore be attributed to these two parasites.

Since most of the chalcidoid activity took place prior to August 17, collections in this locality should be made early in the season to obtain the maximum number of *Platygaster herrickii*.

In Kansas conditions were more favorable for avoidance of multiple parasitism, as most of the hosts parasitized by this species occurred on the small, nonproductive culms beneath the surface of the soil where they were not easily accessible to puparial parasites.

SUMMARY

Platygaster herrickii occurs as a parasite of the hessian fly throughout most of the winter-wheat-growing sections of the United States. It is an important parasite in the more southern parts of the eastern wheat-growing sections, in the central wheat belt west of the Mississippi, and in western Oregon.

The adult is from 1.5 to 2.2 mm long and is black and shining.

The egg is deposited in the egg of the host, where it develops simultaneously with that of the host. It is hyaline, subellipsoidal, and about 0.06 mm long at the time of deposition. Its development takes place monembryonically, and at the time of hatching numerous spherical pseudogerms are released into the body cavity of the host, where they become generally distributed.

The primary larva, at time of hatching, is about 0.29 mm long, of cyclopean type, and has a bifurcate caudal extremity. Later in its development it becomes swollen and nearly spherical. The mature larva is white, shining, about 2 mm long, segmented, and reniform. While in this stage it consumes the host contents, but not before the dark puparium of the hessian fly has been formed.

The cocoon is formed within the puparium of the host. It is ovoid and made of thin, elastic, straw-colored material. It is about 2.5 mm long and 1.1 mm wide.

There is one generation a year. The adult hibernates within the cocoon and emerges in the spring at the time the hessian flies are ovipositing. Embryological and larval development proceeds with the development of the host until the end of summer, when the cocoon is formed and pupation is begun. The adult stage is reached before winter.

In Abingdon, Va., heavy mortality has been found to take place in the course of the season, owing chiefly to multiple parasitism.

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OBSERVATIONS ON THE BIOLOGY OF THE WHEAT-STEM MAGGOT IN KANSAS[1]

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INTRODUCTION

The wheat-stem maggot, *Meromyza americana* Fitch (Diptera Chloropidae) is widely distributed through the wheat-growing area of North America. In infested fields it is not uncommon to find from 10 to 15 percent, and in some instances almost 100 percent, of the plants injured by this insect.

REVIEW OF LITERATURE

The literature on the wheat-stem maggot consists largely of short notes in annual reports and various periodicals.

Lugger (*20, Bull. 43, pp. 210–213*)[3] reported that the wheat-stem maggot had been found as early as 1821 in Pennsylvania, but the earliest record in the entomological literature is that of Fitch (*5, p. 299*), who in 1856 described the fly from material collected in New York and gave it the name *Meromyza americana*. Walsh and Riley (*24*) and Riley and Fuller (*22*) reported it as occurring in Missouri. Lintner (*18, 19*) noted its occurrence in New York and included notes on the nature of the injury, the larval and pupal forms, and the time of appearance of the fly. Webster (*25, pp. 389–390*), in Ohio, reported finding a full-grown larva in a stem of wheat on June 14; on June 16 a larva was found in the upper joint of a growing straw; on June 24 puparia were collected; and on July 18 he observed the copulation of emerged adults. He also reported the frequent occurrence of the mite *Heteropus ventricosus* Newport as a parasite of the maggot. Forbes (*9*) reported the maggot in Illinois and described the immature stages of the insect. He also collected and described the parasite *Coelinius meromyzae*. Forbes (*10*) contributed notes on the life history of the maggot and suggested the probability of a midsummer brood in self-sown grain, making a total of three broods each year. Fletcher (*6*) reported injury in both spring and fall in Canada, and the collection of a specimen of hymenopterous parasite thought to be a new species or a variety of *Coelinius meromyzae* (Forbes).

Webster (*26*) found the wheat variety Velvet Chaff to be more highly infested with the wheat-stem maggot than Michigan Wonder. Garman (*14*) reported the occurrence of the insect in Kentucky,

[1] Received for publication Nov. 30, 1936; issued August 1937. Contribution no. 447 from the Department of Entomology, Kansas Agricultural Experiment Station. This work was conducted at the field insectary and agronomy farm, Manhattan, Kans., in connection with project 8, The Hessian Fly and Other Wheat Insects.

[2] The authors are indebted to Dr. John H. Parker and Dr. H. H. Laude, of the Department of Agronomy, for suggestions and plant materials; to Prof. D. A. Wilbur, of the Department of Entomology, for collection records, and to other members of the Department of Entomology for suggestions and helpful criticisms; to Dr. H. Morrison and other members of the Division of Insect Identification, Bureau of Entomology and Plant Quarantine, U. S. Department of Agriculture, for identification of parasites; and to C. W. Sabrosky for identifications of *Meromyza* and records of its distribution in Kansas.

[3] Reference is made by number (italic) to Literature Cited, p. 237.

where it was especially common in blue-grass pastures, even when closely grazed. Fletcher (*7*) stated that *Agropyron divergens* Nees (awned bluestem) was badly injured by the maggot. Osborn and Gossard (*21*) recorded the occurrence of the maggot in Iowa and reported it as being preyed upon by the parasite *Coelinius meromyzae* Forbes and by two other undetermined species of parasites. Webster (*27, pp. 74–79*) spoke of it as being possibly the most widely distributed of all wheat-stem worms.

Lugger (*20, Bull. 43, pp. 210–213*) reported the insect in Minnesota, and recorded evidence which indicated the presence of three generations. Later (*20, Bull. 48, p. 38*) he reported it as damaging late-sown rye, to the extent of 10 percent. Williams (*30, pp. 17–20*) noted its presence in South Dakota. Fletcher (*8*) stated that there were three broods of flies at Ottawa, Canada.

Bruner and Swenk (*1, pp. 24–26*) reported the maggot as being distributed throughout Nebraska. Three broods were recorded, the fall brood usually attacking the grain most severely. Wheat planted in October seemed to be less liable to attack than that sown earlier.

Criddle (*3, pp. 236–237*) collected flies on *Agropyron repens* (L.) Beauv. and *A. occidentalis* Scribn. Cooley (*2*) reported the maggot as injuring wheat in Montana.

Kelly (*17*) reported the laying of eggs by the parasite *Coelinidae meromyzae* within the eggs of *Meromyza americana*. His report states that the parasite eggs hatch within the eggs of *Meromyza* and the young larvae feed within the fatty tissue of the wheat-stem maggots without disturbing their vital processes, emerging as adults from the puparia of *Meromyza*.

Webster (*28*) found the insect in North Dakota but stated that "blighted" heads in wheat may also be due to the foot rot disease. He found the maggot attacking slender wheatgrass (*Agropyron tenerum* Vasey), wild barley (*Hordeum jubatum* L.), and pigeon grass (*Chaetochloa glauca* Scribn.).

One of the best publications on the wheat-stem maggot is that of Gilbertson (*15*). He described the injury produced, recorded the life history of the insect, and described its immature stages. He also gave a list of host plants and furnished information on the control of the pest by a hymenopterous parasite, *Microbracon meromyzae* (Gahan). Gilbertson found an undetermined species of mite attacking the adult flies and an unidentified fungus on dead maggots.

The distribution of *meromyza americana* in Kansas has been given by Sabrosky (*23, p. 216*).

MATERIALS AND METHODS

Detailed studies of the life history of the wheat-stem maggot under Kansas conditions were begun in the fall of 1932. Adult flies were collected and caged on young plants of Turkey wheat (*Triticum aestivum* L., syn. *T. vulgare* Vill.) in the field. These cages were observed daily for evidence of mating and deposition of eggs. After eggs had been deposited the plants were dissected, and the sections bearing eggs were placed in small shell vials and observed daily for evidence of the first hatching. These sections of plants were later examined for young maggots, some of which were preserved for study and others for use in rearing experiments.

The major portion of the life-history studies was carried on in 1933. During the last week of March, maggots secured from clumps of volunteer wheat were placed inside of sections of fresh wheat stems from which the centers had been removed. Each of these sections with the included maggot was placed in a small shell vial in the bottom of which had been packed a thin layer of moist, sifted soil. Each vial was tightly corked, numbered, and recorded. Moisture was added to the soil at frequent intervals to keep the humidity within the vials high, a condition which appeared to be most favorable for the maggots.

In addition to the maggots collected from volunteer wheat, others were collected from winter wheat, spring wheat, barley, rye, and grasses and given similar treatment. Maggots were also reared from eggs secured from the oviposition tests. In all, some 500 maggots were carried through partial or complete life cycles. Of this number, 156 were reared from eggs, and the remainder were collected from various sources and in various larval instars, or as puparia.

Maggots of various stages, eggs, and puparia were preserved for study and measurement. The exuviae from maggots and the cephalopharyngeal skeletons of dead maggots were mounted in Canada balsam on microscopic slides and studied to determine the differences in various instars and to provide the specimens for the drawings of the cephalopharyngeal skeletons.

Early in April sweepings were begun to determine the date of first appearance of the flies. The flies collected in these sweepings were used in the oviposition tests.

In infested fields "blasted"[4] heads appear shortly before harvest (fig. 1, *D*). During the first 2 weeks of June, all of the blasted heads were collected from the wheat variety plots and the date-of-planting-variety plots at the agronomy farm. In making the collections the culms were cut near the crown of the plant so that the entire culm was preserved. The culms from each plot were tied in separate bundles, labeled, and placed in large cardboard boxes, from which the flies were collected as they emerged from the culms. These boxes were closed to the light except for two round holes near the top of one end of each, into which common lamp chimneys were inserted. The outer ends of the chimneys were closed to prevent the escape of the flies as they emerged. A little water was sprayed over the wheat at frequent intervals to insure sufficient moisture for the emerging flies. The boxes were examined daily, and the flies and other insects removed. The sex of each *Meromyza* fly was determined, and any Hymenoptera that might be parasites of *M. americana* were preserved for identification.

After most of the flies had emerged, each of the culms was split lengthwise to determine how many of those having blasted heads had been infested by stem maggots. Of 6,527 culms examined in 1933, 99.9 percent of the blasted heads were due to *Meromyza* injury.

The adult flies from the sweepings and those reared from the culms having blasted heads were used in oviposition tests. Some of the flies were caged in pairs, and others were caged several together on small wheat plants in pots. Common lamp chimneys with cloth tops were used for cages in these experiments in the field insectary. Other

[4] "Blasted" heads are heads which appear white and ripen prematurely with stiff, spreading awns, presenting a striking contrast to the green of the leaves and of the normal heads.

FIGURE 1.—Life stages of and damage produced by the wheat-stem maggot: *A*, Adult female. × 15. *B*, Egg in normal position. × 10. *C*, Maggot in feeding position where central shoot is severed, resulting in blasted heads as shown in *D*. × 3. *D*, Spring type of injury showing blasted heads (*a*) and normal heads (*b*). × ½. *E*, Fall type of injury showing injured tillers, (*a*) and a normal tiller (*b*). × ½.

flies were caged on young wheat growing out of doors. A cage 3 feet square and 1 foot high was used in these outdoor experiments. The primary purpose of the outdoor experiments was to secure large numbers of eggs. In all these experiments records were kept of the number of eggs deposited and the position of the eggs on the plants. These records were compared with those taken on egg-deposition habits in the field.

From time to time records have been made of the infestation of different wheat varieties by the wheat-stem maggot. These counts were made on winter wheats, in the following seasons: Spring of 1921, fall of 1924, 1927, 1931, 1932, and 1933. In each of these variety tests the same number of plants was examined for each variety in the test. This number, however, varied in the different tests, and this variation should be considered in the interpretation of the data.

LIFE HISTORY

ADULT

Meromyza americana may be distinguished from others of its family (Chloropidae) by the fact that the costa extends only to the third vein, and by the greatly enlarged hind femora and the correspondingly curved tibiae (fig. 1, *A*). The flies are slender and pale green to yellow. They are almost devoid of bristles or hairs, with three broad, grayish-black stripes on the mesonotum, three brown to black stripes (which often coalesce) on the dorsum of the abdomen, the antennae slightly infuscated above, and the front almost entirely destitute of hairs except for a few on the orbits and on the lateral margins of the triangle. The second and third veins of the wing are conspicuously curved forward, the latter ending some distance before the apex of the wing. A full technical description is given by Forbes (*9*).

Flies that have recently emerged are pale green in color, but as they grow older the color turns to pale yellow or straw. The eyes vary from a bright green to a deep bronze which variation is probably due to the age of the fly.

The difference in the appearance of the flies of the two sexes is largely in the size, the male being much smaller. The abdomen of the female fly is rounded and swollen, while that of the male is more or less cylindrical, tapering gradually to a dull point.

Soon after the flies emerge from the puparia they begin to mate. Mating may take place at any time during the first few days after emergence, and a single female has been observed mating more than once either with the same or with a different male.

The ratio between the sexes of *Meromyza americana* was determined by examination of 2,149 flies reared from June 10 to June 18. Of these 1,180, or slightly more than half, were females, the ratio being 55 percent females to 45 percent male.

From records kept on 10 females the preoviposition period was found to vary from 2 to 6 days, and the average was 3.6.

EGG

The eggs are snow white, and are fusiform-cylindrical in shape with gently rounded ends. On the anterior extremity is a minute, flattened, rounded area. The surface is covered with longitudinal ridges, the spaces between the ridges being concave and marked off into

rectangular areas by smaller transverse ridges (fig. 1, *B*, and fig. 2, *A*). From measurements made of 50 eggs the length was found to range from 0.96 to 1.09 mm, and the greatest breadth from 0.165 to 0.231 mm. The average length was 1.02 mm and the average breadth 0.194 mm (table 1).

TABLE 1.—*Measurements of the various immature stages of the wheat-stem maggot*

Item	Egg (50 individuals)		(25 individuals) first instar		(25 individuals) second instar		(50 individuals) third instar		(44 individuals) puparium	
	Length	Breadth	Length	Breadth	Length	Breadth	Length	Breadth	Length	Breadth
	mm	*mm*	*mm*	*mm*	*mm*	*mm*	*mm*	*mm*	*mm*	*mm*
Maximum	1.09	0.231	1.86	0.57	3.31	0.66	6.47	1.21	5.86	1.10
Minimum	.96	.165	1.61	.31	3.05	.34	6.21	.96	5.54	.82
Average	1.02	.194	1.75	.45	3.20	.50	6.40	1.10	5.70	.91

On the young plant the eggs of the wheat-stem maggot are usually deposited singly either on the leaves or on the leaf sheaths, but in a few instances eggs were found between the leaf sheath and the stem. In the fall a great many eggs are found glued to the stem just above the ground. In the oviposition experiments carried on in the insectary the majority of the eggs were glued to the upper surface of the leaves a short distance from the stem. In most cases the eggs were parallel to the long axis of the leaves and stem (Fig. 1, *B*).

Since the eggs are laid singly and the oviposition period extends over several days it is difficult to estimate the number of eggs laid by a single individual. In cage experiments an average of 10 to 15 eggs were deposited by each female. The largest number deposited by a single female was 30. The eggs were deposited at an average rate of one to four daily. One female, under cage conditions, deposited 13 eggs in a single day. The length of the oviposition period ranged from 4 to 10 days and the average was 6.91 days.

TABLE 2.—*Length of stages of the wheat-stem maggot*

Item	Oviposition period of adult (32 individuals)	Incubation period (31 individuals)	First instar (42 individuals)	Second instar (26 individuals)	Third instar (16 individuals)	Entire larvae stage	Period in puparium (46 individuals)	Egg to adult	Adult (13 individuals)
	Days	*Days*	*Days*	*Days*	*Days*	*Days*	*Days*	*Days*	*Days*
Maximum	10	11	11	28	[1] 23	[1] 62	20	[1] 82	19
Minimum	4	4	2	2	9	13	5	18	2
Average	6.91	6.80	6.19	11.25	14.56	32.10	11.72	43.82	9.38

[1] Does not include overwintering larvae.

The incubation period varied from 4 to 11 days, with an average length of 6.8 days (table 2).

LARVA

The full-grown larva is an active, slender, glassy, pale-green maggot, tapering anteriorly and to some extent posteriorly (fig. 1, *C*). The hooks, which are typical of muscoid larvae, are found beneath the

head and serve to differentiate it from most other larvae that infest wheat except those of the same group. A more complete description has been given by Forbes (*9*).

It was found in these experiments that the larvae pass through three instars. When first hatched they are very small, slender, and white, with neither a head capsule nor feet. Twenty-five newly hatched larvae were measured, and the average length was found to be 1.75 mm and the average width 0.45 mm (table 1).

The larvae of the second instar are somewhat larger than those of the first instar, and are of a very light whitish-green color. Of 25 such larvae measured the average length was 3.20 mm and the average width was 0.50 mm (table 1).

Fifty larvae of the third or last instar were measured and the average length was found to be 6.40 mm and the average width 1.10 mm (table 1). Forbes' (*9*) description was evidently made from specimens of this instar.

From the suckerlike mouth, located on the under surface of the first segments, usually protrudes a pair of black-toothed hooks, the mandibles (fig. 2, *C*). These are supported by and connected to the cephalopharyngeal skeleton, which is a V-shaped structure extending back into the body as far as the third segment. The cephalopharyngeal skeleton is a brownish or blackish scleritized structure and is usually visible through the integument of the larva. It differs in shape in the different instars. In the third instar it is completely developed and the parts are easily distinguished. The skeleton of this instar is represented in Figure 2, *F*, which shows the mandibular, hypostomal, and pharyngeal sclerites and the small arched dentate sclerite completely developed, with the small accessory sclerites attached to the hypostomal sclerite. The dentes on the mandibular sclerite are fully developed and completely scleritized.

The cephalopharyngeal skeleton of the second-instar larva is represented in figure 2, *E*. This skeleton is similar to that of the third instar, except that it is smaller and the dentes are not fully developed or scleritized.

The cephalopharyngeal skeleton of the first-instar larva is represented in figure 2, *D*. This skeleton differs greatly from that of either of the other instars. Not only is it materially smaller, but it is also less completely developed. The dentate sclerite and the two small accessory sclerites are completely absent and the dentes of the mandibular sclerite are poorly developed. The mandibular sclerite is not heavily scleritized as it is in the skeletons of the other two instars.

The first of the three larval instars was found to require a period of from 2 to 11 days, the average being 6.2 days; the second instar required from 2 to 28 days, the average being 11.4 days; the third required from 9 to 23 days, the average being 14.6 days. The entire larval stage therefore required from 13 to 62 days, or an average of 32.1 days (table 2). These results do not include overwintering larvae.

These calculated results from partial life histories, when compared with the results obtained from eight cases in which the larvae were actually reared from egg to adult, were found to be both higher and lower, but the average time was similar. The length of the three instars in the eight actual tests varied from 16 to 40 days, the average time being 27.4 days.

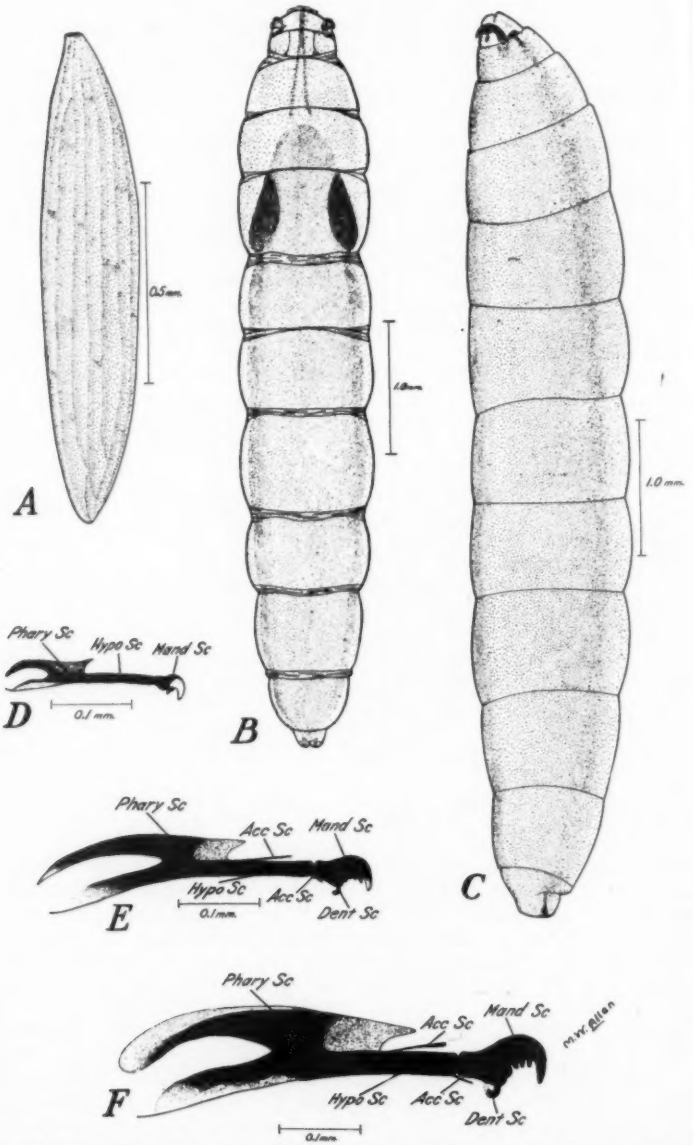

FIGURE 2.—Characteristics of the immature forms of *Meromyza americana*: *A*, Egg; *B*, puparium; *C*, full-grown larva; *D*, cephal opharyngeal skeleton of first-instar larva; *E*, cephalopharyngeal skeleton of second-instar larva; *F*, cephalopharyngeal skeleton of third-instar larva. *phary* Sc, pharyngeal sclerite; *hypo* Sc, hypostomal sclerite; *mand* Sc, mandibular sclerite; *dent* Sc, dentate sclerite; *acc* Sc, accessory sclerite.

PUPA

The pupa forms inside of the last larval skin or puparium, where it may be seen through the semitransparent larval skin. The constrictions between the segments are more marked than in the larva and the puparium is more yellowish in color (fig. 2, *B*). Forbes (*9*) has given a full description of this stage.

Forty-four puparia were measured, and the average length was found to be 5.7 mm and the average width 0.9 mm (table 1). Figure 2, *B*; shows a typical puparium.

The period from the formation of puparia to the emergence of adults varied from 5 to 20 days; the average being 11.7 days (table 2). The time from hatching of the egg to emergence of the adult, calculated from the foregoing results, varied from 18 to 82 days, the average being 43.8 days (table 2). These results were checked against the records of four maggots reared from egg to adult. The four records showed a variation in time from 42 to 57 days with an average of 46.3 days. These figures, both calculated and recorded, are for the spring and summer generations and do not take into consideration the overwintering brood.

SEASONAL CYCLE

From the rearing experiments and from field observations, in the vicinity of Manhattan, the cycle for the year 1933 was determined (fig. 3). The data for 1933 probably represent about the normal for this locality.

The insects overwintered as full-grown larvae which pupated during the latter part of March and the first half of April. The adults began to emerge on April 15 and continued to emerge throughout April and the first half of May. These adults mated within a few days after emergence and deposited their eggs during the latter part of April and through the greater part of May. The eggs began to hatch about the last of April, and the larvae were found in the stems of wheat, rye, and barley throughout May. They pupated about the last of May and in early June. The adult flies emerged from these puparia from June 5 to June 28. The flies of this generation deposited their eggs during the latter part of June, and the larvae emerged from the eggs from June 25 to the last of July. These larvae fed within the stems of wild and cultivated grasses. They pupated from the middle of July until August 8, and the adults emerged until about the middle of August.

Eggs were deposited by this third brood of flies during the latter part of July and the first half of August. The maggots from these eggs emerged during the last few days of July and throughout the greater part of August. They lived in the stems of grasses and volunteer wheat. Many became full-grown larvae, passed the winter in that stage, and pupated the following spring. Some of the larvae from these eggs, however, pupated during August and emerged as adults during the latter part of that month. Adults were present in the field until December 16. These adults, which had emerged during August, September, and the first part of October, deposited eggs that hatched before October 15, the larvae overwintering and pupating the following spring. Thus there is evidence of three full generations and a partial fourth in Kansas.

FIGURE 3.—Life cycle of *Meromyza americana*, 1933.

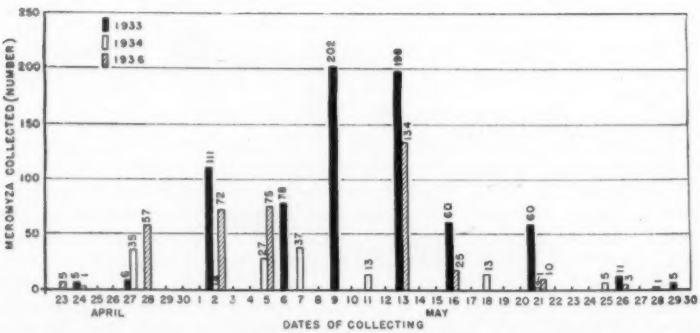

FIGURE 4.—Collection records showing abundance of adults of *Meromyza* during the spring of 1933, 1934, and 1936; these collections were made on grass plots near the wheat plots used in the differential infestation tests.

NATURAL CHECKS

During these experiments 18 species of Hymenoptera were reared, 4 of which were from puparia of *Meromyza americana;* 3 others were from culms of blasted heads, and 11 others were from volunteer wheat known to be heavily infested by the wheat-stem maggot. Table 3 shows nine species which are recorded in literature as parasitic upon *Meromyza.* Only one of these, *Euphoriana uniformis* Gahan, was not reared during these studies. The names of the parasites are listed under their family designations in table 3, with the sources from which reared, the number reared, and literature citations to previous records of their parasitism on *Meromyza.*

Coelinidea ferruginea was described by Gahan (*11*) from three specimens, two females and one male reared by C. N. Ainslie at Elkpoint, S. Dak., the type locality. The host was *Meromyza americana.* All the parasites of this species which were reared during the present experiments were from puparia of overwintering larvae or, in May and June, from the puparia from which the first brood of flies normally emerge.

TABLE 3.—*Hymenopterous parasites of the wheat-stem maggot*

Parasite	Parasites reared from—			Recorded in literature as parasite of *Meromyza*
	Puparia of wheat-stem maggot	Culms having blasted heads infested by maggot	Volunteer wheat infested by maggot	
	Number	*Number*	*Number*	
Ichneumonoidea:				
Alysiidae:				
Coelinidea ferruginea Gahan	10		13	Gahan (*11*).
Coelinidea meromyzae (Forbes)	4		1	Forbes (*9*).
Braconidae:				
Euphoriana uniformis Gahan [1]				Gahan (*11*).
Microbracon mellitor (Say)		1		
Microbracon meromyzae (Gahan)	3	10		Do.
Microplitis melianae Vier		3		
Meteorus vulgaris (Cress.)			1	
Ichnumonidae:				
Casinaria scabriformis Vier			1	
Proctotrupoidea:				
Platygasteridae:				
Leptacis sp			1	
Chalcidoidea:				
Eulophidae:				
Horismenus texanus (Girault)			3	Gahan (*13*).
Notaniomorpha meromyzae (Gahan)			9	Gahan (*12*, p. 226).
Eupelmidae:				
Eupelmus allynii French			2	Gahan (*13*).
Eurytomidae:				
Eurytoma tylodermatis Ashm		1		
Mymaridae:				
Polynema striaticorne Girault			2	
Pteromalidae:				
Bubekia fallax Gahan			15	Do.
Callitula bicolor Spinola			1	Do.
Eupteromalus fulvipes (Forbes)			7	
Halticoptera aenea (Walk.)			1	
Cynipoidea:				
Figitidae:				
Hypodiranchis sp	1		14	

[1] Not reared during these experiments.

Coelinidea meromyzae was described (*9*) from specimens reared from *Meromyza americana* and from specimens collected in the vicinity of Cuba, Ill. Kelly (*17*) gives detailed biological observations on this species. In the present work four specimens were reared in July from puparia produced by maggots of the second generation. The fifth specimen was reared from volunteer wheat in the greenhouse, January 10, probably from a puparium of an overwintering maggot.

Microbracon meromyzae (Gahan) was described by Gahan (*11*) from six specimens, three females and three males, reared by C. N. Ainslie at Elkpoint, S. Dak. A male specimen was also reared by J. A. Hyslop at Hagerstown, Md. The host in both cases was *Meromyza americana*. The three specimens of this species which were reared during the writers' experiments were from puparia formed in late May, early June, and in July. Ten others were reared from the culms of blasted heads.

Hypodiranchis sp. has not previously been reported as attacking the wheat-stem maggot, and, according to L. H. Weld, appears to be an undescribed species. In fact, no species of *Hypodiranchis* seems to have been described from North America; the genotype *H. hawaiiensis*, and most of the known species of the genus were described by William Ashmead from the Hawiian Islands. A related European species *Cothonaspis rapae* (Westd.) has been reported by James (*16*) as parasitic on the cabbage-root maggot (*Hylemyia brassicae* Bouche.). One specimen of *Hypodiranchis* was reared from a single puparium collected June 9, and 14 others were reared from volunteer wheat during October, November, December, and January. Those reared from volunteer wheat probably came from puparia formed by overwintering maggots which matured early under greenhouse conditions.

Other Hymenoptera reared from volunteer wheat or from blasted heads infested by *Meromyza* are listed in table 3. These records show the presence of these species in Kansas and suggest the possibility that some are parasitic on the wheat-stem maggot there, especially where they have previously been reported as parasitic on this insect.

In addition to the hymenopterous parasites of *Meromyza americana* reared during the present experiments, one other has been recorded in the literature. This species, *Euphoriana uniformis*, was described by Gahan (*11*) from the male type reared from *M. americana* by J. A. Hyslop at Hagerstown, Md., and from the female type collected by W. H. Menke at Garden City, Kans.

Frequently reference is made in the literature to a small mite *Pediculoides ventricosus* Newport, which is reported as killing the larvae by sucking their blood. This mite is not known to occur in Kansas.

Many times, both in the rearing experiments and in the field, brown or partially brown larvae were found. They seemed to die slowly, and when the integument was ruptured the internal organs were found to be decayed and liquid. This condition was probably brought about by bacteria.

A fungus determined by C. L. Lefebvre as *Cladosporium* sp. was often found associated with the dead maggots. Most of the species of this genus are saprophytic, although a few are parasitic. This one is probably a saprophyte, but until the species is determined, no definite statement can be made concerning it.

FEEDING HABITS OF THE INSECT AND NATURE OF INJURY TO WHEAT

Upon emerging from an egg the larva makes its way to the point where the central leaf or head-bearing shoot emerges from its investing sheath. Upon reaching this point it works its way down between the sheath and the central shoot, girdling the latter as it progresses downward to its final feeding position, which is at the base of the culm in fall and early spring, and just above the upper node in late spring and summer. The larva enters the central shoot and there does most of its feeding. It feeds by tearing the plant tissues with its mandibles and sucking the juices from the lacerated tissue. Before the larva enter the central shoot the feeding takes place between this shoot and its investing sheath.

When first entering the plant and during the migration down to the feeding position, the larva feeds with its head down, but when the feeding position in the center of the culm is reached this position is reversed, and the greater part of the feeding is done with the anterior end up (fig. 1, *C*).

Two types of injury are produced by the wheat-stem maggot, one in late spring and summer, the other in autumn and early spring. In late spring and summer the larva destroys the lower part of the stem, thus preventing the normal flow of sap to the head of the plant. The head dries prematurely and the kernels, if present at all, are small, shriveled, and unfit for food or planting. When this type of injury occurs the head and central shoot are light straw color rather than green like those of uninfested stems. The awns are stiff, brittle, and spreading, and do not extend upward from the glumes as in normal plants (fig. 1, *D*).

In the fall and early spring the larva attacks the central shoot (fig. 1, *E*), cuts the vascular bundles, and so prevents the flow of the sap into the upper part of the leaf. This injury may be of considerable importance. In some cases the entire tiller turns yellow and dies. After injuring or killing one tiller the larva may migrate to a fresh one. In laboratory experiments the larvae have sometimes been found to migrate from an injured tiller to a fresh one on another plant. These plants have always been in close proximity, however, and no records are available to show the distance that larvae may migrate. Larvae placed on the soil near plants have, with few exceptions, been able to reach the plants and feed within them.

A serious aspect of this autumnal and early spring type of injury is that the larvae which cause the injury to heading wheat later in the spring are produced by flies that emerge from this earlier generation of larvae.

FOOD PLANTS

During the experiments wheat-stem maggots were observed feeding within the stems of the following species of plants:

Common bread wheat (*Triticum aestivum* L.).
Durum wheat (*Triticum durum* Desf.).
Triticum vulgare × *T. durum* (from various sources).
Triticum macha Va.
Triticum persicum stramineum Zhuk.
Triticum timopheevi Ahuk.

Barley (six-row) (*Hordeum vulgare* L.).
Rye (*Secale cereale* L.).
Timothy (*Phleum pratense* L.).
Yellow bristlegrass (*Setaria lutescens* (Weigel) F. T. Hubb.).
Green bristlegrass (*Setaria viridis* (L.) Beauv.).

In addition to these food plants the maggot has been reported in the literature as feeding within the stems of:

Emmer (*Triticum dicoccum* Schrank).
Quackgrass (*Agropyron repens* (L.) Beauv.).
Slender wheatgrass (*Agropyron pauciflorum* (Schwein.) Hitchc.).
Bluestem (*Agropyron smithii* Rydb.).
Bluebunch wheatgrass (*Agropyron spicatum* (Pursh and Smith) Scribn.
Foxtail barley (*Hordeum jubatum* L.).
Canada wild-rye (*Elymus canadensis* L.).
Smooth bromegrass (*Bromus inermis* Leyss.).
Japanese chess (*Bromus japonicus* Thunb.).

Meromyza americana has not been found feeding on oats.

DIFFERENTIAL INFESTATION OF VARIETIES

RELATION OF STAGE OF PLANT MATURITY TO NUMBER OF HEADS BLASTED BY *MEROMYZA*

Some evidence of the presence in wheat varieties of resistance to injury from the wheat-stem maggot has been presented by Dunham (*4*) and by Gilbertson (*15*). The number of blasted heads collected in the various 1/40-acre plots of varieties of winter wheat at the agronomy farm [5] are given in table 4. In all cases the number of infested culms collected from each plot is but a small proportion of the total number of heads present. The relative numbers, however, indicate considerable differences among the varieties represented. These differences may be due (1) to differences in the dates of heading and maturity of the several varieties in relation to the peak number of second-generation adults present and laying eggs, or (2) to varietal differences in palatability or attractiveness to the insect giving rise to actual resistance.

Additional data bearing on this question have been secured from a date-of-planting experiment involving four varieties. These varieties, Early Blackhull, Quivira, Kanred, and Oro, were planted on several dates at intervals of approximately 1 week. The varieties studied in 1933, the dates of planting, and the number of blasted heads collected, together with other information to be discussed later, are given in table 5. The marked differences in each variety in the number of blasted heads formed on plants from the various dates of planting are shown in figure 5, *A*. According to figure 5, *A*, and table 5 Oro planted October 5, Kanred planted October 11, Quivira planted October 18, and Early Blackhull planted October 25, produced the greatest number of blasted heads.

[5] These plots, used in yield tests, are under the supervision of Dr. H. H. Laude, to whom the authors are indebted for permission to collect the material and for data on dates of heading, maturity, and other agronomic characters.

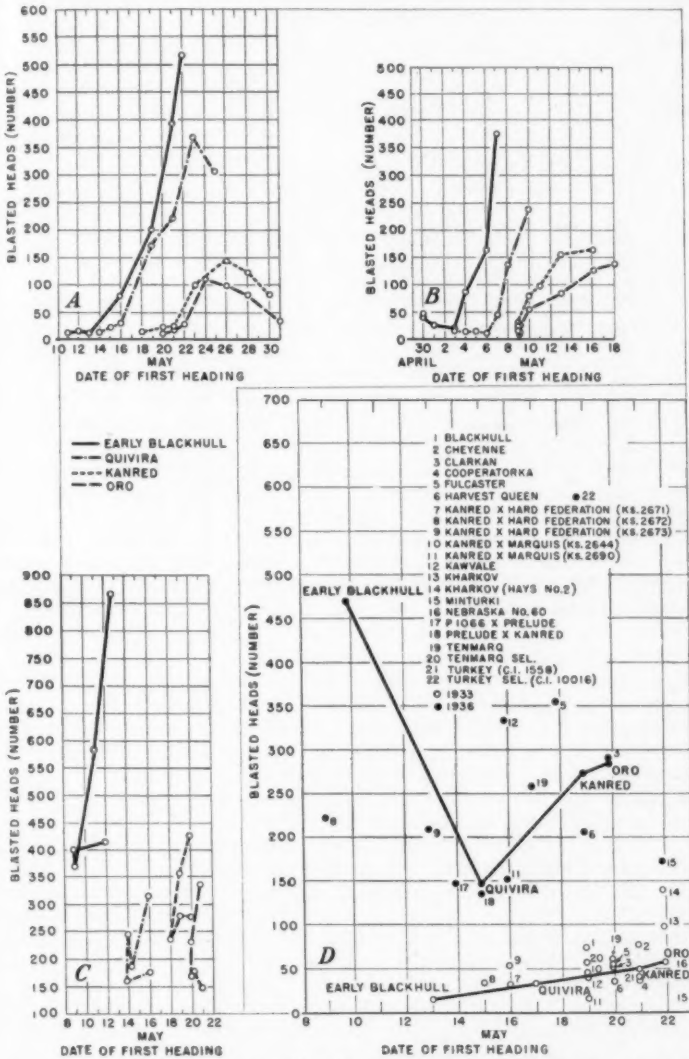

FIGURE 5.—Relation between the number of blasted heads and the datesof first heading for various varieties of wheat in 1933 (*A*), 1934 (*B*), 1936 (*C*), and 1933 and 1936 (*D*).

TABLE 4.—*Relative number of blasted heads produced in wheat varieties by the wheat-stem maggot, spring 1933* [1]

Rank	Kansas no.	C. I. no.[2]	Variety	Date of first heading, May 1933	Blasted heads per 1/40-acre plot				
					Series			Total infested	Average infested
					1	2	3		
					Number	*Number*	*Number*	*Number*	*Number*
1	483	8856	Early Blackhull	13	27	10	9	46	15.3
2	2690	11589	Kanred × Marquis	19	24	9	15	48	16.0
3	2464	6156	Minturki	23	23	21	8	52	17.3
4	2671	11373	Kanred × Hard Federation	16	9	21	64	94	31.3
5	2628	8886	Quivira	17	49	10	36	95	31.7
6	2672	10091	Kanred × Hard Federation	15	40	13	50	103	34.3
7	10	6199	Harvest Queen	20	43	39	22	104	34.7
8	499	8861	Cooperatorka	21	32	63	16	111	37.0
9	570	1558	Turkey	21	39	29	47	115	38.3
10	2593	8180	Kawvale	19	45	38	35	118	39.3
11	2644	10090	Kanred × Marquis	19	44	32	57	133	44.3
12	2401	5146	Kanred	21	50	46	51	147	49.0
13	322	6250	Nebraska no. 60	23	50	69	34	153	51.0
14	505	8858	Clarkan	20	67	57	30	154	51.3
15	317	6471	Fulcaster	20	53	51	55	159	53.0
16	2673	10092	Kanred × Hard Federation	16	73	21	65	159	53.0
17	2670	10089	Tenmarq Selection	19	51	44	69	164	54.7
18	495	8220	Oro	22	43	68	------	111	55.5
19	514	6336	Tenmarq	20	67	73	34	174	58.0
20	343	6251	Blackhull	19	39	89	87	215	71.7
21	2667	8895	Cheyenne	21	32	58	135	225	75.0
22	2591	1442	Kharkof	22	65	139	80	284	94.7
23	2650	6686	Kharkof (Hays no. 2)	22	88	185	------	273	136.5

[1] Heads collected from variety plots of the agronomy farm; varieties planted Sept. 28, 1932.

[2] C. I. denotes accession number of the Division of Cereal Crops and Disease, Bureau of Plant Industry, U. S. Department of Agriculture.

An attempt was made to correlate these differences with other associated facts. Several factors, such as date of emergence of plants, date of first heading, date fully ripe, stand per acre, number of culms per acre, yield, length of fruiting period, plant height, test weight per bushel, rainfall, and temperature were considered. The closest correlation was found between the amount of injury and the date of first heading.[6] Those plots marked "first heading" between May 22 and May 26 had a larger number of blasted heads than those heading either before or after that date. Those plots marked "first heading" after the date of maximum infestation were one plot of Quivira, two plots of Kanred, and three plots of Oro (table 5).

From the data obtained it appears probable that the stage of growth of the plants at the time of oviposition by the flies is important. Apparently in late spring some specific stage in the maturity of the plants is more acceptable to the female flies or is more palatable to the larvae than are other stages of maturity.

In studying another problem Wilbur and Sabrosky (*29*) found the maximum number of adult *Meromyza* on pasture grass less than one-quarter of a mile away from the wheat plots during the period from May 9 to 13. This is 13 days earlier than the date of first heading which marked the maximum infestation in wheat. The period involved is somewhat longer than the average number of days required for incubation of eggs. Apparently the data give an indication of the length of the interval between egg deposition and the time at which the young larvae cause the appearance of blasted heads. This peak of insect emergence, shown in figure 4, appears to be part of the explanation of the differences in infestation associated with different dates of planting.

The figures given do not take into account the number of culms that might have been missed in the count in cases in which the injury took place so early that no part of the blasted head appeared beyond the top leaf sheath. In some of the culms collected the heads were well exserted; in others part of the head was enclosed in the leaf sheath. In each culm collected from these date-of-planting variety plots the distance from the base of the head to the top of the leaf sheath was measured, and the average distance and the percentage of heads completely exserted were calculated (table 7).

These data show differences from plot to plot and between varieties. They also indicate a difference in infestation of nonfruiting culms which should be investigated.

It appears from the data in table 5 that the date of maturity of a variety is one factor but not the only one involved in the differences in infestation by *Meromyza*. For example, there were 379 infested culms in the seven plots of Oro as compared to 1,232 in the plots of Early Blackhull. But the plots of Oro included three which headed after the one with maximum infestation, as well as the three which headed before May 24, while all the plots of Early Blackhull headed before the date which gave the maximum infestation in the case of

[6] First heading is the date when about 10 percent of the plants have headed.

TABLE 5.—*Effect of date of planting and variety of wheat on late spring injury by the wheat-stem maggot in 1933*

Variety	Kansas no.	Blasted heads per 1/40-acre plot and date of first heading of wheat planted—														Total blasted heads
		Sept. 14		Sept. 23		Sept. 28		Oct. 5		Oct. 11		Oct. 18		Oct. 25		
		Number		*Number*		*Number*		*Number*		*Number*		*Number*		*Number*		*Number*
Early Blackhull	483	13	May 11	17	May 12	13	May 13	80	May 16	200	May 19	393	May 21	[1] 516	May 22	1, 232
Quivira	2628	15	May 14	24	May 15	31	May 16	171	May 19	221	May 21	[1] 366	May 23	305	May 25	1, 133
Kanred	2401	16	May 18	23	May 20	24	May 21	98	May 23	[1] 146	May 26	123	May 28	82	May 30	512
Oro	495	10	May 20	20	May 21	28	May 22	[1] 110	May 24	93	...do....	83	...do....	35	May 31	379

[1] Plot in which maximum infestation occurred.

TABLE 6.—*Effect of date of planting and variety of wheat on late spring injury by the wheat-stem maggot in 1934*

Variety	Kansas no.	Blasted heads per 1/40-acre plot and date of first heading for wheat planted														Total
		Sept. 16		Sept. 22		Sept. 29		Oct. 6		Oct. 13		Oct. 20		Oct. 27		
		Number		*Number*		*Number*		*Number*		*Number*		*Number*		*Number*		*Number*
Early Blackhull	483	47	Apr. 30	41	Apr. 30	26	May 1	19	May 3	87	May 5	164	May 7	375	May 8	759
Quivira	2628	17	May 3	16	May 4	15	May 5	10	May 6	45	May 7	137	May 8	237	May 10	477
Kanred	2401	14	May 9	22	May 9	29	May 9	79	May 10	97	May 11	153	May 13	151	May 16	555
Oro	495	12	May 9	10	May 9	24	May 9	53	May 10	84	May 13	125	May 16	135	May 18	443

the other varieties. If the experiment had included plots of Early Blackhull heading at a time comparable to those of Oro, the difference in infestation in favor of Oro might have been much greater.

TABLE 7.—*Average percentage of exserted heads from infested culms collected in date-of-planting variety test and length of peduncle,*[1] *1933*

Date of planting	Oro		Kanred		Quivira		Early Blackhull	
	Percent	Length	Percent	Length	Percent	Length	Percent	Length
		Mm		*Mm*		*Mm*		*Mm*
Sept. 14	40	+16	37	−4	57	+42	46	+14
Sept. 23	38	+3	35	−9	43	+19	65	+42
Sept. 28	50	+9	59	+18	77	+57	85	+54
Oct. 5	52	[2] +14	44	−2	67	+37	76	+40
Oct. 11	8	−41	18	[2] −24	54	+13	76	+47
Oct. 18	18	−26	14	−37	32	[2] −12	56	+13
Oct. 25	11	−36	16	−33	30	−20	66	[2] +33

[1] Measured from base of head to top of the infesting leaf sheath; +=heads extending above leaf sheath, −=heads not surpassing leaf sheath.
[2] Plot in which maximum infestation occurred.

The data from these date-of-planting plots indicate that the relative position of Early Blackhull as the variety with the lowest infestation in table 4 is not in accord with the potentialities of this variety. They indicate further that it is necessary to consider the date of first heading in the respective varieties in interpreting the relative resistance of the varieties. Thus a number of the late-maturing wheats appear to have the highest infestation. But Minturki, which headed within the period indicated as the one in which the highest infestation took place, is probably the most resistant of the wheats listed and perhaps materially better than Oro.

Data collected on these same plots in the abnormally dry season of 1934 (table 6) tend to confirm the results discussed above. The growing season of 1934 was one in which the early plant development was greatly accelerated. All plots of a given variety headed earlier in 1934 than plots of the same variety in 1933. On the other hand, insect development was not so greatly accelerated. The peak of emergence of *Meromyza*, according to the data of Wilbur and Sabrosky (*29*), occurred about May 5 to 7, only about 4 to 6 days earlier than in 1933. This difference between insect and plant development in the 2 years appears to have resulted in a reduction in the difference in total number of blasted heads between the varieties with high and low infestations. There are no plots of any of the varieties which headed later and in which the number of blasted heads was below the maximum per plot for the variety. The rank of the varieties in respect to the plots of maximum infestation in 1934 (table 6) was the same as in 1933 (table 5). The curves (fig. 5, *B*) from the data were also similar to the parts of the curves for the earlier plots of the year 1933 (fig. 5, *A*). The similarity between the results of the 2 years indicates that the differences between the varieties are significant.

TABLE 8.—*Relative number of blasted heads produced in wheat varieties by the wheat-stem maggot, spring 1936* [1]

Rank	Kansas no.	C. I. no.	Variety	Date of first heading, May 1936	Blasted heads per 1/40-acre plot				
					Series			Total infested	Average infested
					1	2	3		
					Number	Number	Number	Number	Number
1	2689	11591	Prelude× Kanred	15	58	209	------	267	133.5
2	2628	8886	Quivira	15	100	168	162	430	143.3
3	2695	11590	P1066 × Prelude	14	94	194	------	288	144.0
4	2690	11589	Kanred × Marquis	16	------	148	------	148	148.0
5	2464	6156	Minturki	22	168	------	------	168	168.0
6	19	6199	Harvest Queen	19	201	------	------	201	201.0
7	2673	10092	Kanred × Hard Federation	13	------	230	183	413	206.5
8	2672	10091	Kanred × Hard Federation	9	197	306	159	662	220.6
9	514	6936	Tenmarq	17	254	------	------	254	254.0
10	2595	8220	Oro	20	280	------	------	280	280.0
11	2401	5146	Kanred	19	196	407	207	810	270.0
12	505	8858	Clarkan	20	284	------	------	284	284.0
13	2593	8180	Kawvale	16	336	318	330	984	328.0
14	317	6147	Fulcaster	18	443	252	------	695	347.5
15	483	8856	Early Blackhull	10	278	587	508	1,373	457.6
16	2720	10016	Turkey	18	------	579	------	579	579.0

[1] Heads collected from variety plots of the agronomy farm; varieties planted Oct. 1, 1935, except Minturki, planted Oct. 2, and Oro planted Oct. 4, 1935.

TABLE 9.—*Effect of date of planting and variety of wheat on late spring injury by the wheat-stem maggot in 1936*

Variety	Kansas no.	Blasted heads per 1/40-acre plot and date of first heading for wheat planted—										Total
		Sept. 13		Sept. 20		Sept. 30		Oct. 4		Oct. 11		
		No.		No.		No.		No.		No.		No.
Early Blackhull	483	464	May 12	452	May 9	419	May 9	633	May 11	916	May 13	2,884
Quivira	2628	226	May 16	210	May 14	294	May 14	237	May 14	365	May 16	1,332
Kanred	2401	325	May 20	327	May 19	286	May 18	405	May 19	476	May 20	1,819
Oro	495	198	May 21	227	May 20	219	May 20	280	May 20	385	May 21	1,309

The lower infestation in 1933 in plots first heading after May 26 may indicate a stage in the growth of culms in which they are more acceptable to the fly for oviposition or more palatable to the young larva. Observations made in earlier years on date-of-planting plots containing the single variety Kanred showed an infestation similar to that on plots of this variety in 1933.

Additional counts of blasted heads in variety and variety-date-of-planting plots were made in 1935 and 1936. The early spring of 1935 was dry, but this was followed by a period of wet weather when the wheats were heading. Some varieties, especially the early ones, sent up a second growth of heads which were heavily infested by *Meromyza*. During the latter part of the time in which blasted heads were being collected it became impossible to distinguish such heads from the earlier matured normal heads. For this reason collection was discontinued before harvest. However, the data secured give further indication of a relation between stage of plant maturity and infestation.

Data secured from counts of blasted heads made in 1936 are recorded in tables 8 and 9 and figure 5, *C, D*. Data on abundance of *Meromyza*

are given in figure 4. The dates of first heading of the plots studied are more nearly comparable to those in 1934 than to those in 1933, while the reverse is true of the abundance of *Meromyza*, which appeared in numbers earlier and reached a peak later in 1936 than in 1934. This may have influenced the total number of blasted heads collected.

Some peculiarity of the season of 1936 caused one or more of the earlier planted plots to reach the stage of first heading after some of the later planted ones. In general the number of blasted heads shows a closer relationship to date of first heading than to date of planting, thus giving further evidence of the relation of stage of plant maturity to infestation by *Meromyza*.

The type of season also resulted in bringing the date of first heading for the different dates of planting much closer together than usual, as is indicated in table 10. There is some evidence that the type of season had a different effect on different varieties. Taking these facts into consideration, the data from the variety-date-of-planting plots in 1936 are reasonably similar to those secured in 1933 and 1934.

TABLE 10.—*Range in number of days from earliest date of first heading to latest date of first heading for each of four varieties tested in date-of-planting-variety plots during 1933, 1934, and 1936*

Variety	Range in days		
	1933	1934	1936
Early Blackhull	11	8	4
Quivira	11	7	2
Kanred	12	7	2
Oro	11	9	1
Total range of all varieties	20	18	12

In the variety series (table 8) the relative infestation of early maturing varieties in general is somewhat different from that of 1933 under a lighter infestation. Especially is this true of the relationship of Early Blackhull and Quivira to the other varieties. On the other hand, Minturki still retains its position with the lowest infestation when the period of first heading is taken into consideration. Four varieties heading at an earlier date than Minturki had a lower infestation but were not exposed to the maximum oviposition. Hence, throughout these spring infestations there is evidence that both variety and stage of maturity are important in determining the amount of injury.

The results of both variety and date-of-planting tests indicate the value of an early maturing variety or early maturity in the lessening of damage by the spring brood of the wheat-stem maggot.

FALL INFESTATIONS

From a summary of counts of maggot infestation made during several years previous to 1934 it was found that some varieties of wheat appeared to have less of the fall and early-spring type of injury than did other varieties. Among 80 varieties and strains of wheat studied in two or more tests there was a range of from 0 to 29 in the average percentage of plants infested. Most of the varieties having a low infestation had been in a very few tests in which the intensity

of the infestation was low on all varieties. Hence these low figures are considered to be of doubtful significance. The intensity of infestation in the different years, as indicated by the average infestation, varied from 2.8 to 32.6.

From among this group of wheats the 21 varieties recorded in table 11 have been selected for presentation because they were studied in five or more tests or were of particular interest in connection with the study of the late spring infestation.

TABLE 11.—*Infestation of winter-wheat varieties by the fall generation of "Meromyza americana" in various years between 1924 and 1933*

Kansas no.	C. I. no.	Variety	Early spring 1921, 25 plants	Fall 1924, 15 plants	Fall 1927, 20 plants	Fall 1931, 60 plants	Fall 1932, 50 plants	Early spring 1933, 25 plants	Fall 1933, 50 plants	Average infestation of—	
										Variety named	Turkey in same tests
			Per cent	*Per cent*	*Per cent*	*Per cent*	*Per cent*	*Per cent*	*Per cent*	*Per cent*	*Per cent*
2522	6161	Honor	-------	0.0	0.0	10.0	8.0	0.0	-------	3.6	13.8
2564	3342	Dawson	-------	.0	10.0	3.5	10.0	.0	-------	4.7	13.8
19	6199	Harvest Queen	24.0	6.8	.0	4.0	-------	.0	-------	6.9	20.6
439	6936	Tenmarq	-------	6.8	5.0	4.0	4.0	.0	28.0	9.1	17.8
2448	6155	Minturki	-------	.0	15.0	-------	12.0	-------	14.0	10.3	24.8
2672	10091	Kanred×Hard Federation	-------	-------	-------	13.0	6.0	5.9	28.0	10.7	13.0
2401	5146	Kanred	-------	7.2	8.9	2.5	2.0	4.0	44.0	11.4	17.8
435	6163	Shepherd	-------	6.8	10.0	25.0	18.0	.0	-------	12.0	13.8
223415	------	Illini Chief Selection	-------	9.2	8.8	1.3	6.0	8.0	44.0	12.9	17.8
2667	8885	Cheyenne	-------	-------	-------	14.1	8.0	.0	30.0	13.0	13.0
483	8856	Early Blackhull	-------	-------	-------	25.8	10.0	.0	20.0	13.9	13.0
2132	------	Red Winter	28.0	.0	30.0	14.0	12.0	4.0	-------	14.7	18.2
2628	8886	Quivira	-------	-------	-------	25.4	8.0	.0	26.7	15.0	13.0
2993	8180	Kawvale	-------	-------	15.0	1.9	22.0	8.0	28.0	15.0	16.8
2588	5338	Imperial Amber	-------	33.3	10.0	14.0	6.0	12.5	-------	15.2	13.8
495	8220	Oro	-------	-------	-------	-------	12.0	.0	34.0	15.3	16.0
2594	8257	Fulhard	-------	-------	30.0	9.3	10.0	8.0	28.0	17.1	16.8
	5566	Beechwood	32.0	13.3	25.0	20.0	14.0	.0	-------	17.4	18.2
343	6251	Blackhull	-------	-------	12.3	13.8	12.0	10.5	44.0	18.5	16.8
359	5597	Red Rock	-------	.0	25.0	40.0	12.0	4.5	32.0	18.9	17.8
570	1558	Turkey	40.0	40.0	15.0	4.0	6.0	4.0	38.0	21.0	21.0
		Average	32.6	7.1	13.1	11.5	7.8	2.8	32.3	-------	-------

A few varieties, such as Turkey, Red Rock, Blackhull, and Beechwood, were rather consistently high in all tests. Other varieties, such as Honor, Dawson, Harvest Queen, Tenmarq, and Minturki, were usually below the average in all tests.

It is of interest that the variety Minturki, which showed little infestation by the late-spring brood, also showed relatively little infestation by the fall brood. The varieties Oro, Kanred, Quivira, and Early Blackhull, studied in the date-of-planting series are not arranged in the same ranking under the two infestations. From the small differences between varieties and the erratic behavior in the different years it is questionable whether the low fall varietal infestation here indicated is of economic importance. However, additional tests under more uniform infestation may show differences of importance.

SUMMARY

In the life history of *Meromyza americana* Fitch there are three larval instars which are distinguishable by the shape of the cephalopharyngeal skeleton. The total life cycle is completed in from 18

to 82 days in the summer. The winter is passed in the larval stage. At Manhattan, Kans., there are three generations and a partial fourth each year.

During the course of these experiments four parasite, *Coelinidea ferruginea* Gahan, *C. meromyzae* (Forbes), *Microbracon meromyzae* (Gahan), and *Hypodiranchis* sp., were reared from purparia of the wheat-stem maggot. Eighteen species of Hymenoptera, including these four, were reared from volunteer wheat or culms heavily infested by the wheat-stem maggot. Nine species known to be parasitic on *Meromyza* are recorded in the literature.

In the fall and early spring the wheat-stem maggot kills the central leaf of the plant destroying the tiller on which it feeds. The white or blasted heads which appear at heading time result from the feeding of the larva above the upper node.

The wheat-stem maggot has been recorded as feeding on several species of *Triticum* on barley, rye, and on a number of native and introduced grasses.

Plants from later sown seeds were more heavily infested in the spring than plants from earlier sowings. Differences in resistance to infestation were noted among the different wheat varieties tested. These differences may not be of economic importance but further study should be made under more frequent and heavier infestations.

The data collected from the variety and date-of-planting plots indicate that there is a stage in the growth of the plant which is more palatable to the larva or more attractive to the female fly than are other stages of growth.

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